

Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology.

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SYNOPSIS. Relationships of lacertid lizards were assessed on the basis of 84 primary and 112 binary characters drawn mainly from morphology, including features of the skeleton, external anatomy, various internal soft part systems and two aspects of behaviour. Among features not previously used, or not fully investigated before, are structure of the septomaxilla and nasal passages, arrangement of the xiphisternal cartilages, mite pockets, kidney

position, ulnar nerve arrangement, thoracic fascia, aspects of the hemipenis and its associated muscles, female genitalia and jaw muscles. On the basis of parsimony analysis and compatibility treatment of this character set, the Lacertidae fall into two main portions: a paraphyletic Palaearctic and Oriental group of primitive forms, from which is derived a holophyletic assemblage of Ethiopian and advanced Saharan and Eurasian taxa.

The former group is not fully resolvable, but *Psammodromus* and *Gallotia* appear to be sister groups and are probably related to *Lacerta parva* and *L. fraasi* and then *L. brandtii*. *Podarcis* appears to be related successively to *L. andreanszkyi*, the sister species *L. dugesi* and *L. perspicillata*, and perhaps *L. danfordi* and *L. laevis*. This assemblage may be related to archaeolacertas and *Algyroides*. The separation of *Lacerta lepida*, *L. pater* and *L. princeps* from the *L. agilis* group, based on chemical evidence, is weakly contradicted by morphology. *Takydromus* may be most closely related to *L. vivipara*, and *Lacerta jayakari* and *L. cyanura* constitute the most likely sister group of the Ethiopian and advanced Saharo-Eurasian assemblage.

Taxa in the Ethiopian and advanced Saharo-Eurasian assemblage form a long essentially pectinate tree with relatively minor change between the side branches, except for a strong disjunction separating the more primitive from the more advanced taxa. Most of the former fall on two main branches, with '*Lacerta*' *australis* and '*L.*' *rupicola* possibly basal to them. 1. the Equatorial forest group containing *Gastropholis*, *Bedriagaia*, '*Lacerta*' *echinata*, *Adolfus*, '*Lacerta*' *jacksoni* and *Holaspis*. The first three of these constitute a holophyletic group and the same is probably true of the remainder. 2. *Tropidosaura*, *Poromera* and *Nucras*, the latter being the sister group of the more advanced forms. These include successively the Ethiopian *Philochortus*, *Latastia*, *Ichnotropis* and *Heliobolus*, *Pseuderemias*, *Meroles* and *Aporosaura*, and *Pedioplanis*, and then the Saharo-Eurasian *Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops-Cabrita*.

It seems probable that the ancestors of modern Lacertidae arose in western Eurasia, where the family is known since the Palaeocene and is still represented there largely by quite primitive forms (89 species and seven nominal genera). The family later invaded Africa, perhaps first in the early or middle Miocene. Relatively primitive lacertids spread widely in largely mesic situations in the Ethiopian region, radiating to some extent (six present genera and 16 species) and producing *Nucras* and the related series of advanced groups (eight genera and 54 species) which show increasing adaptation to xeric environments. These genera tend to have their most primitive species in the northeast and north of the Ethiopian region. The most advanced gave rise to the Saharo-Eurasian clade, now made up of *Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops-Cabrita*. This invaded the arid areas of North Africa and Eurasia, where it is presently represented by 70 species. Many morphological changes in increasingly advanced lacertids may be functionally related to the problems of survival in arid, hot, open environments. Considerable ecological parallelism exists in lacertids, with members of separate stocks occupying similar niches in different geographical areas. Morphological adaptations associated with these niches contribute significantly to the high levels of character homoplasy found in the family. There is also some correlation between the degree of niche differentiation in various groups and the quality of the phylogenies that can be produced from their physical characters. A number of morphological parallels exist between advanced lacertids and New World macroteiids. In the skull at least, advanced lacertids show a complex mixture of paedomorphosis and acceleration.

Nomenclatorial changes are as follows: *Cabrita* is synonymised with *Ophisops*, necessitating a new name, *Ophisops nictans*, for *Cabrita jerdonii*. *Aporosaura* is synonymised with *Meroles*, *Platyplacopus* with *Takydromus*, and *Bedriagaia* with *Gastropholis*. '*Lacerta*' (or *Centromastix*) *echinata* is also transferred to the latter genus and *Lacerta jacksoni* to *Adolfus*. '*Lacerta*' *australis* and '*L.*' *rupicola* are put in a new genus, *Australolacerta*. It is recommended that *Lacerta dugesi* and *L. perspicillata* should not be placed in the otherwise very uniform genus *Podarcis*. Although clearly paraphyletic, *Lacerta* s. lat. should be retained at least for the present and, if necessary, putative relationships within it indicated by informal groups or subgenera.

INTRODUCTION

The Lacertidae are one of the few large or medium-sized families of lizards not to have been subjected to some form of overall phylogenetic analysis in recent years. The last general treatment was that of G. A. Boulenger (1920, 1921) in his monumental *Monograph of the Lacertidae** which was based almost entirely on external features of the lizards. As these seem to be subject to considerable parallel evolution, I have attempted to widen the available character base by including features of the skeleton and various soft-part systems, such as the nasal tract, kidney, jaw and cloacal muscles, hemipenis and female genitalia. Some of these features have also been

discussed elsewhere (Arnold, 1973, 1983, 1984, 1986a, 1986b, 1986c). Julien and Renous-Lécuru's (1972) work on the ulnar nerve is incorporated and extended and two behavioural characters are included. Recent investigations in the fields of karyology and the immunology and electrophoresis of blood and tissue proteins are also considered. Analysis has been carried out using 112 binary characters and 44 taxonomic units that are likely to be holophyletic. These have been subjected to both parsimony and compatibility treatments.

There are over 230 species of lacertid lizards, presently assigned to about 27 genera (see p. 211). They are distributed through most of Eurasia and all of Africa. A few species occur on some off-shore islands, including the British Isles, the Canaries, Madeira, many Mediterranean islands, Socotra, Sri Lanka, Sumatra, Borneo and Java, Taiwan, the Japanese archipelago and Sakhalin, but not Madagascar. Most of the islands are continental in origin or close to other areas occupied by lacertids, suggesting that these lizards are not particularly good transmarine dispersers (compared with, for instance, geckoes and skinks). Body size is usually small, in most cases less than 120mm from snout to vent and down to

* This was Boulenger's last task in a long and highly productive career. Even before the second volume of the monograph left the press, he quit the field, retired from the British Museum and returned to his native Belgium where he devoted his last years to studying roses. Anyone who has spent much time wandering in the confusing labyrinths of lacertid systematics will tend to sympathise.

33mm in *Ophisops beddomii*, but a couple of species sometimes reach 210mm and a Pleistocene form in the Canaries attained an estimated total length of 1200mm (Bravo, 1953). The majority of forms are ground-dwelling in a range of open and partly closed habitats, but a number climb on rock faces and among vegetation. Lacertids occur from tundra and high mountain habitats through heath, scrub and Mediterranean associations to tropical forest, semi-desert and desert. All species are essentially diurnal and all that have been checked appear to be heliotherms, even ones confined to rain forest. Most lacertids feed mainly on arthropods but some species of *Gallotia* are almost entirely vegetarian, at least when adult. The majority of lacertids appear to be active hunters but some use a sit-and-wait strategy to a considerable extent, for instance *Meroles suborbitalis* and *Pedioplanis lineocellata* (Pianka, Huey and Lawlor, 1979). All, except most *Lacerta vivipara* and three species of *Eremias*, lay eggs (1 – 25 per clutch), the exceptions bearing fully formed young. In many respects, the Lacertidae are a conservative family including no forms with reduced limbs, eyes or ears, no nocturnal or aquatic species and few food specialists; nor do they have distinctive complex morphological adaptations, like the adhesive pads of geckoes, or the specialised tongues of chameleons.

DISTINCTIVE FEATURES OF THE LACERTIDAE

Snout narrow, premaxilla single, nasals paired, maxilla usually contacting frontal dorsally and separating nasal from prefrontal, frontals paired or fused in adults, parietal bone single with anterior tabs but without lateral downgrowths, supratemporal processes of parietal long and parietal table may extend backwards, pineal fontanelle present in most cases, fronto-parietal suture usually showing at least some interdigitation, postorbital and postfrontal bones separate or fused, the latter roofing the supratemporal fossa, supratemporal bone present; lachrymal present, forming lower border of orbit with jugal which may have a quadratojugal process; vomers paired, pyriform recess (interpterygoid vacuity) narrow; pterygoid teeth present or absent; alar process long to very reduced, posterior opening of vidian canal at basisphenoid-prootic suture; cranial osteoderms present and fused with skull bones when in contact with them, palpebral ossifications usually extensive. All mandibular elements present and Meckel's groove open, coronoid overlapping dentary labially; teeth pleurodont, usually bicuspid laterally, occasionally with more cusps. Nearly always 14 scleral ossicles in each eye; hyoid apparatus with ceratohyal and first and second ceratobranchial cartilages.

Presacral vertebrae vary from 22 to 33, females having a higher average number than males in nearly all species; usually three short and two long pairs of nuchal ribs; typically three pairs of ribs attaching to the sternum and two to the xiphisternum; last presacral vertebra sometimes lacking ribs. Clavicle usually expanded medially and perforated to form a continuous or posteriorly interrupted loop, interclavicle cruciform, sternum with a fontanelle in most cases, usually 0, 1 or 2 pairs of inscriptional ribs, rarely 3. Proximal autotomic caudal vertebrae with either one or two pairs of transverse processes, if two then posterior pair may be short and parallel to anterior one or long and diverging posteriorly.

Limbs unreduced, tail cylindrical; head covered by large symmetrical plate-like scales (Fig. 12), a collar (transverse posteriorly directed skin-fold on underside of neck covered externally by large scales) often present, belly scales large, femoral pores usual. Ulnar nerve superficial ('lacertide') or deep ('varanide'), dorsal muscles of the lower hind leg innervated by peroneal nerve (Julien & Renous-Lécure, 1972). Jaw muscles characterised by a bodenaponeurosis divided into two lobes caudally and a parasagittal vertical sheet connecting the quadrate aponeurosis to the temporal fascia (fide Rieppel, 1980). Cloacal muscles usually with a well defined posterior section of the m. transversus perinei (Arnold, 1984). Tongue quite deeply notched. Abdominal fat body often largely outside peritoneum; either lobes of hemipenis completely invested by m. retractor penis magnus, or lobes complexly folded and a complex hemipenial supporting structure, the armature, usually present.

Of these features, the lack of parietal downgrowths, usual presence of sexual variation in number of presacral vertebrae, fat-body position, hemipenial characteristics and perhaps the jaw muscle characters are largely or wholly restricted to the Lacertidae, at least among the Scincomorpha. Within the Lacertoidea, lacertids are further distinguished by closure of the temporal fenestra by the postfrontal.

RELATIONSHIPS OF THE LACERTIDAE

Camp (1923) placed the Lacertidae in the Lacertoidea within the Scincomorpha, along with the Teiidae sensu lato and the Gerrhosauridae (= subfamily Gerrhosaurinae of the Cordylidae). Relationship between the Lacertidae and Teiidae sensu lato has long been suggested (Underwood, 1971), for instance by Boulenger (1920) and has recently been argued by Estes, De Queiroz & Gauthier (1988), who treat these assemblages as sister groups which are successively related to the Xantusiidae, forming the Lacertoidea, and to the Scincoidea (Scincidae plus Cordylidae) to make up the Scincomorpha. Maclean (1974) divided Teiidae, as generally understood, into the subfamilies Teiinae, for the macroteiids, and Gymnophthalminae, for the microteiids. Subsequently, Estes (1983a) raised the latter group to family level, as did Presch (1983). Presch suggested it was the sister group of the Lacertidae but, as shown by Harris (1985), there is no evidence for this relationship in the form of synapomorphies.

Possible synapomorphies of Lacertidae and Teiidae plus Gymnophthalmidae (mainly from Estes, De Queiroz & Gauthier, 1988) are narrow snout and pyriform recess, interdigitating frontoparietal suture usually between prominent parietal tabs, adductor fossa widely open, heterodont dentition, often some caudal vertebrae with two pairs of transverse processes, tongue quite deeply notched, m. transversus perinei frequently with a differentiated posterior section.

TAXONOMIC UNITS USED IN ANALYSIS

Because a total phylogenetic analysis of over 230 species would be difficult, most have been combined into working units that are likely to be holophyletic (i.e. containing all the

descendant species of a single ancestral one). In many cases, these units are recognized genera, but genera may be grouped or divided if there are reasons for believing they are not necessarily holophyletic as they stand. Ideally, holophyly is assumed because the members of the group concerned possess one or more unique derived characters (synapomorphies). In fact, holophyly sometimes has to be inferred from a combination of other indicators, such as close overall resemblance or serial resemblance among species, possession of a distinctive combination of derived features that, while not individually unique, are uncommon elsewhere, and a continuous geographical range. These indicators may also give additional support to holophyletic groups discerned on the basis of apparent synapomorphies.

In the following account, the number of recognised species in a taxonomic unit is given in parentheses and these are then listed. They are followed by any features that are unique to the group or nearly so, its geographical range, and references to any recent taxonomic studies that may be relevant. Hemipenial features mentioned are explained elsewhere (Arnold, 1986a).

Acanthodactylus (28): *arabicus*, *aureus*, *blanfordii*, *boskianus*, *boueti*, *cantoris*, *erythrurus*, *felicis*, *gongrorhynchatus*, *grandis*, *guineensis*, *haasi*, *hardyi*, *longipes*, *maculatus*, *masirae*, *opheodurus*, *orientalis*, *pardalis*, *robustus*, *savignyi*, *schmidtii*, *schreiberi*, *scutellatus*, *spinicauda*, *tilburyi*, *tristrami*, *yemenensis*.

First upper labial scale broad above but with sides converging downwards (Fig. 13c).

Range: Saharo-Sindian region, from Spain and North Africa through Middle East to Northwest India.

Salvador (1982); Arnold (1983).

Adolfus africanus etc (2): *africanus*, *vauereselli*.

Only four complete longitudinal rows of ventral scales.

Range: Equatorial Africa from Cameroon to Uganda, eastern Zaire and western Tanzania.

Arnold (1989).

Adolfus alleni

Range: mountains of Uganda and west Kenya above 2700m.

Arnold (1989).

Algyroides (4): *fitzingeri*, *marchi*, *moreoticus*, *nigropunctatus*.

Lips on hemipenis very small.

Range: Southern Europe.

Arnold (1973); Böhme (1981).

Aporosaura: see *Meroles-Aporosaura*.

Bedriagaia (1): *tropidopholis*

Range: Eastern Zaire

Arnold (1989).

Cabrita: see *Ophisops-Cabrita*.

Eremias (23): *acutirostris*, *andersoni*, *argus*, *arguta*, *aria*, *brenchleyi*, *buechneri*, *fasciata*, *grammica*, *intermedia*, *lineolata*, *multiocellata*, *nigrocellata*, *nikolskii*, *persica*, *pleskei*, *przewalskii*, *quadrifrons*, *regeli*, *scripta*, *strauchi*, *velox*, *vermiculata*.

Rostral scale narrowed with sides sloping inwards and downwards towards mid-line (also present in *Meroles reticulatus*).

Range: Palaearctic region, from eastern Europe and Turkey to China and adjoining USSR and south into Iran and Pakistan.

Shcherbak (1974).

Gallotia (4): *atlantica*, *galloti*, *simonyi*, *stehlini*.

Forty chromosomes (Cano, Baez, Lopez-Jurado & Ortega, 1984); no sexual variation in number of presacral vertebrae (approached by a few species of *Acanthodactylus*); dark chevrons frequent on throat.

Range: Canary Islands.

Böhme & Hutterer (1985).

Gastropholis (2): *prasina*, *vittata*.

Range: Coastal Kenya, Tanzania and Mozambique.

Arnold (1989).

Heliobolus (5): *lugubris*, *neumanni*, *nitida*, *quadrinasalis*, *spekii*.

Range: Africa south of the Sahara desert.

Holaspis (1): *guentheri*

Maxilla not contacting frontal dorsally, only 12 scleral ossicles in each eye, extra fontanelle in scapulocoracoid; frontoparietal scales fused to each other and to interparietal, lateral dorsal body scaling transversely expandable, tail depressed with lateral fringes of pointed scales.

Range: Equatorial Africa from Sierra Leone south to Angola and thence eastwards to Tanzania, Mozambique and Malawi.

Arnold (1989).

Ichnotropis (7): *bivittata*, *capensis*, *chapini*, *grandiceps*, *microlepidota*, *squamulosa*, *tangicana*.

Coarse plication on basal parts of hemipenial lobes.

Range: Southern Africa north to Congo, Zaire and Tanzania.

Lacerta agilis group (7): *agilis*, *media*, *pamphylica*, *schreiberi*, *strigata*, *trilineata*, *viridis*

Range: Europe, central and southwestern Asia.

Peters (1962a), Arnold (1973), Böhme (1984), Schmidtler (1986).

Lacerta andreanszkyi

Range: Atlas of Morocco.

Lacerta – *archaeolacertas* etc (23): *armeniaca*, *bedriagae*, *caucasica*, *clarkorum*, *chlorogaster*, *dahli*, *defilippi*, *derjugini*, *horvathi*, *lantzicyreni*, *mixta*, *monticola*, *mosorensis*, *parvula*, *portschinskii*, *praticola*, *raddei*, *rostombekovi*, *rudis*, *saxicola*, *unisexualis*, *uzzelli*, *valentini*.

Range: Southern Europe, Caucasus and neighbouring South-west Asia.

Darevskii (1967); Bannikov, Darevskii, Ischenko, Rustamov & Shcherbak (1977); Böhme (1984).

'*Lacerta*' *australis* etc (2): *australis*, *rupicola*.

Range: South Africa (Western Cape Province and northern Transvaal).

FitzSimons (1943).

Lacerta brandtii

Range: Northwest Iran and adjoining USSR.

Lacerta cappadocica

Range: East Turkey, North Iraq, Northwest Iran.

Eiselt (1979).

Lacerta danfordi etc. (3): *anatolica*, *danfordi*, *oertzeni*.

Range: Southwest Turkey and offshore islands.

Eiselt & Schmidtler (1987).

Lacerta dugesii

Range: Madeira.

Richter in Böhme (1986).

'Lacerta' echinata

Range: Equatorial Africa from Liberia to eastern Zaire.
Arnold (1989)

Lacerta graeca

Range: Southern Greece.

'Lacerta' jacksoni

Range: mountains of eastern Zaire, Uganda, Kenya and Tanzania.
Arnold (1989).

Lacerta jayakari etc (2): *cyanura*, *jayakari*.

Range: Oman, southeastern Arabia.

Arnold (1972, 1973); Lutz, Bischoff and Mayer (1986).

Lacerta laevis

Range: Southeast Turkey, Syria, Lebanon, Israel, Jordan, Cyprus.

Lacerta lepida etc (2): *lepida*, *pater*.

Range: Southwest Europe, Northwest Africa.

Bischoff (1982).

Lacerta oxycephala

Range: Southwest Yugoslavia.

Lacerta parva etc (2): *fraasii*, *parva*.

Lobes of hemipenis not plicate, but with longitudinal flaps.

Range: Turkey and adjoining USSR; Lebanon.

Peters (1962b); Arnold (1973).

Lacerta perspicillata

Range: Northwest Africa.

Richter in Böhme (1986).

Lacerta princeps

Range: Southeast Turkey to West Iran.

Eiselt (1968, 1969).

Lacerta vivipara.

Range: Europe eastwards across northern Asia to Sakhalin island.

Latastia (8): *boscai*, *carinata*, *cherchii*, *doriai*, *johnstonii*, *lanzai*, *longicaudata*, *taylori*.

Range: Southwest Arabia, Nigeria to Sudan, Somalia, Kenya, Tanzania, Mozambique, Malawi, eastern Zaire, Zambia, Zimbabwe.

Arillo, Balletto & Spanò (1967).

Meroles-Aporosaura (7).

Meroles (6): *ctenodactylus*, *cuneirostris*, *knoxii*, *micropholidotus*, *reticulatus*, *suborbitalis*

Aporosaura (1): *anchietae*

Hemipenial clavulae conjoined at base (not checkable in highly modified hemipenis of *M. suborbitalis*). *Aporosaura* shares many features with advanced *Meroles*.

Range: Coastal Angola, Namibia and western South Africa.

Arnold (in press).

Mesalina (11). *adramitana*, *ayunensis*, *balfouri*, *brevirostris*, *guttulata*, *martini*, *olivieri*, *pasteuri*, *rubropunctata*, *simoni*, *watsonana*.

Clavulae directly attached to hemipenial lobes.

Range: Saharo-Sindian region from North Africa, through Middle East to Northwest India.

Arnold (1986a, 1986 b).

Nucras (7): *boulengeri*, *caesicaudata*, *intertexta*, *lalandii*, *scalaris*, *taeniolata*, *tessellata*.

Exposure of ectopterygoid bone on the side of the skull below maxilla very marked; first three pairs of nuchal ribs with cylindrical terminal cartilages.

Range: Southern Africa north to Kenya, Uganda and Angola.
Broadley (1972).

Ophisops-Cabrita (8)

Ophisops (6): *beddomii*, *elbaensis*, *elegans*, *jerdoni*, *microlepis*, *occidentalis*

Cabrita (2): *jerdonii*, *leschenaultii*.

Huge undivided window in lower eyelid.

Range: North Africa, Southwest Asia, Indian subcontinent.

Arnold (in preparation)

Pedioplanis (11): *benguelensis*, *breviceps*, *burchelli*, *gaerdesi*, *inornata*, *laticeps*, *lineoocellata*, *husabensis*, *namaquensis*, *rubens*, *undata*.

Outer connectors arise very close together on dorsum of hemipenial armature and may fuse (not always apparent in forms with highly modified hemipenes).

Range: Southern Africa north to Angola and Transvaal.

Arnold (in press).

Philochortus (6). *hardeggeri*, *intermedius*, *lhottei*, *neumanni*, *phillipsi*, *spinalis*.

Distinctive hemipenial pattern with peculiar outer connectors; long and short dorsal ribs poorly differentiated.

Range: Southwest Arabia, Somalia, Ethiopia, northern Kenya; scattered relict populations in North Africa.

Platyplacopus: see *Takydromus-Platyplacopus*.

Podarcis (15): *bocagei*, *erhardii*, *filfolensis*, *gaigiae*, *hispanica*, *lilfordi*, *melisellensis*, *milensis*, *muralis*, *peloponnesiaca*, *pityusensis*, *sicula*, *taurica*, *tiliguerta*, *wagleriana*.

Range: Central and southern Europe, Northwest Africa, Northwest Turkey.

Böhme (1986).

Poromera (1): *fordii*.

Hemipenis symmetrical but not bifurcate, with loosely folded walls in retracted organ.

Range: Cameroon, Rio Muni, Gabon, Congo [?].

Psammodromus algirus

Range: Southwest Europe, Northwest Africa.

Very strongly overlapping ventral scales.

Böhme (1981).

Psammodromus hispanicus etc. (3): *blanci*, *hispanicus*, *microdactylus*.

Femoral pores enlarged in inguinal region.

Range: Southwest Europe, Northwest Africa.

Pseuderemias (5). *brenneri*, *erythrosticta*, *mucronata*, *smithi*, *striata*

Four scales round nostril (also present in some *Ophisops*); very narrow snout (also present in *Meroles reticulatus* and *Acanthodactylus masirae*).

Range: Coastal Sudan, Ethiopia, Djibouti, Somalia, northern Kenya.

Takydromus-Platyplacopus (14)

Takydromus (10): *amurensis*, *haughtonianus*, *hsuehshanensis*, *khasiensis*, *sauteri*, *septentrionalis*, *sexlineatus*, *smaragdinus*, *tachydromoides*, *wolteri*.

Platyplacopus (4): *dorsalis*, *intermedius*, *kuehnei*, *sylvaticus*

Lateral teeth with three cusps (shared only with some *Gallotia*); femoral pores well developed but reduced to 1 to 3

on each side; lobes of retracted hemipenis with dorsoventrally compressed or triskelion transverse section.

Range: Japanese archipelago, Taiwan, Korea, adjoining USSR and China westwards to Assam and south to Borneo and Java.

Tropidosaura (4): *cottrelli*, *essexi*, *gularis*, *montana*.

Range: South Africa.

FitzSimons (1943).

Species not considered due to unavailability: *Lacerta mostoufii* Baloutch, (1977), *Eremias ercolinii* Lanza & Poggesi (1975).

DETERMINATION OF CHARACTER POLARITY

There are a number of methods for determining the polarity of characters, that is which state is likely to be primitive in the group under investigation and what its relationships to other states are. Some aspects of this process are discussed elsewhere (Arnold, 1981a) and the indicators used here explained below.

Outgroup analysis

If a character has two or more states within the studied group and one is also widespread in related taxa, that is in outgroups, it is likely to be primitive within the studied group. Successive principal outgroups of the Lacertidae among squamates appear to be Teiidae plus Gymnophthalmidae, Xantusidae, Scincidae + Cordylidae, Anguioidea, Gekkota and Iguania (Estes, De Queiroz & Gauthier, 1988), with the position of snakes and amphisbaenians not precisely determined. Further outgroups among the living tetrapods are *Sphenodon*, other amniotes and amphibians. A state found throughout all these groups is very probably primitive in the Lacertidae, but it is rare for cases to be so unequivocal. Often insufficient information exists about the distribution of states in the outgroups, or states are difficult to recognise with certainty in the more distant ones. Again, it is not uncommon for more than one state to occur in the outgroups, albeit often at different frequencies. Because of these problems, outgroup evidence of primitiveness has been divided into criteria of generally diminishing strength. 1. State widespread in tetrapods or at least lizards. 2. State universal or nearly so in scincomorphs other than lacertids (Teiidae, Gymnophthalmidae, Xantusidae, Scincidae and Gerrhosauridae). 3. State found in majority of scincomorphs other than lacertids. In general, distribution across a range of outgroups, even if the state concerned is absent from the most immediate one, is given more credence as an indicator of primitiveness than presence in the immediate outgroup alone. This is because the latter situation is likely to involve reversal which, in many characters, seems less probable than parallel development in the studied group and its immediate outgroup. 4. State present in primitive members of scincomorph families.

Even in cases where there is a strong and consistent indication of polarity in the outgroups, this method may not always correctly predict the primitive state in the group under consideration. This is especially likely if the character turns out to be very homoplastic in the studied group, so that it is clearly labile and more likely to have reversed in the ancestral stem.

Outgroup techniques within studied group

Outgroup techniques can be used within the studied group, if holophyletic subgroups can be established within it. Thus, if one state of a character is generally widespread and also occurs in a holophyletic subgroup (such as those listed in the previous section) with another state restricted to this, then the latter is likely to be derived. This technique is more powerful once a substantial part of the phylogenetic structure of the group is established. Outgroups can then often be determined for each subgroup concerned and polarity estimated with more certainty for that subgroup, even if the restricted state also occurs in others.

Ontogeny

Appearance first in development is often cited as an indication of primitiveness and quite frequently agrees with other polarity indicators, although conflicts are not uncommon.

Commonality

States that are widespread in the studied group are, on average, more likely to be primitive, although many exceptions to this generalisation are likely.

Presence in most primitive forms

By and large, states found in the most primitive members of a group are more likely to be primitive themselves. Initial analysis establishes an assemblage of primitive forms in the Palaearctic and Oriental regions (p. 230).

Compatibility analysis

The compatibility technique used here (p. 229), which does not involve any prior assumptions of polarity, produces a preferred set of compatible (non-conflicting) characters. Character state distribution within such a set may be represented by a bifurcating diagram joining the taxa (Fig. 1). If

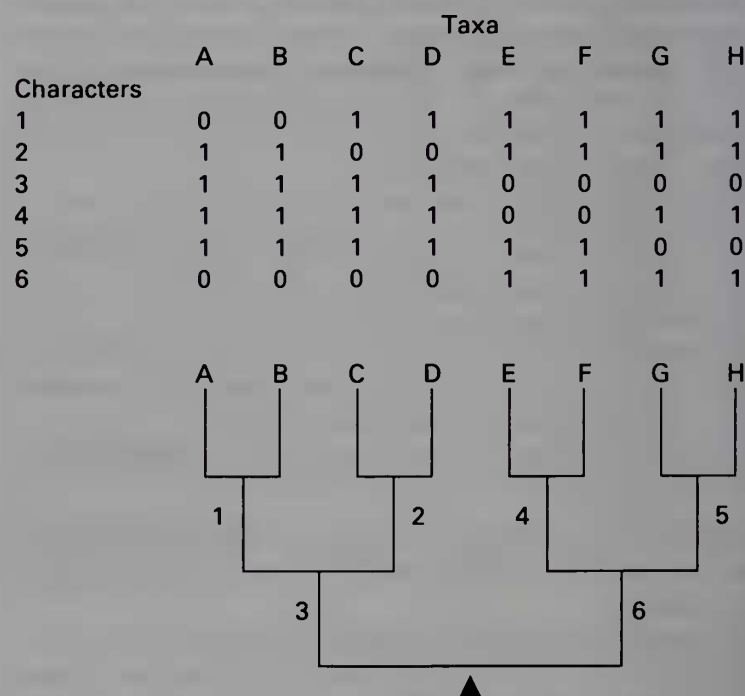


Fig. 1 Hypothetical set of compatible characters for taxa A to H, and a diagram based on the distributions of their states. Figures in diagram indicate where particular states of characters change. ▲ indicates where root subsequently established.

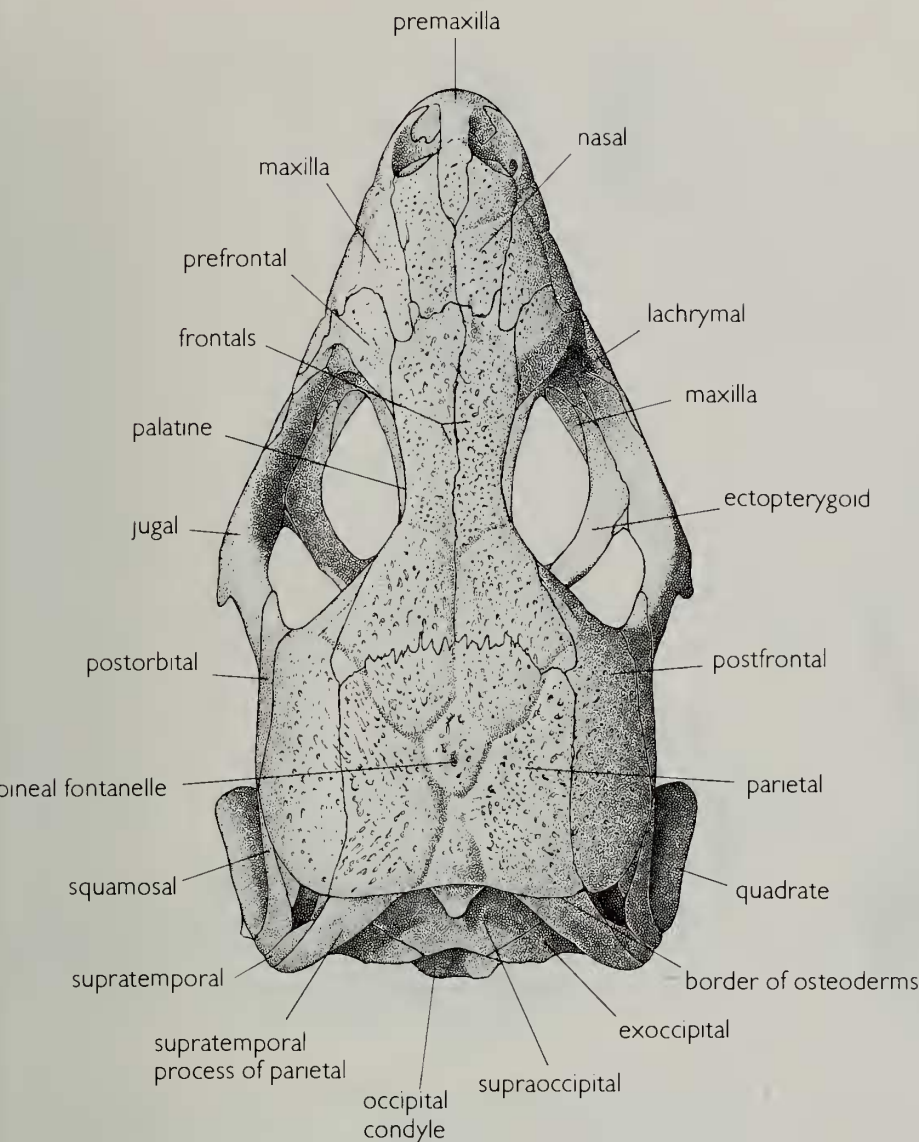


Fig. 2 Skull of primitive lacertid (*Podarcis taurica*), with thick osteodermal layer (crusta calcarea), showing principal dorsal bones.

the polarity of some of the characters is known from other sources, such as outgroup comparison, the diagram can be rooted and converted into a putative phylogeny. It may then be used to retrospectively determine the direction of change of characters of previously unknown polarity. For instance in Fig. 1, if it is known from other sources that the 1 states of characters 3 and 6 are derived, so that taxa A, B, C and D, and E, F, G and H, are likely to be distinct holophyletic groups, then it is clear that the 0 states of characters 1, 2, 4 and 5 are also likely to be derived. The root of the putative phylogeny can consequently be established. Direction of change in such a diagram can also sometimes be confirmed by the distribution of characters that are not in the original compatible set. For instance, if this set specifies an assemblage of taxa that is only part of the studied group, a secondary analysis confined to that assemblage will often produce a larger set of compatible characters for this assemblage, and some of the additional ones may be helpful in determining the direction of character change. Characters that fail to be included in compatible sets because of limited homoplasy can also sometimes be useful in this respect.

In lacertids, compatibility analysis produces a hierarchical pattern of character distribution associating *Lacerta jayakari* (Fig. 19) etc and Ethiopian and advanced Saharo-Eurasian lacertids, and another for *Psammodromus* and its relatives; characters of uncertain polarity in these areas can consequently be resolved, at least provisionally. In the former case,

direction of change is confirmed by the following characters with good polarity indications from other sources: 3, 4, 5, 10, 27, 34, 63 and 81. In the *Psammodromus* series direction is determined by 18, 77, 82 and 83. It should be borne in mind that the *Psammodromus* tree is much less well supported than the one for Ethiopian and advanced Palaearctic lacertids, so polarities partly based on it must be treated with more caution.

The polarity indicators for each character are summarised in Appendix 1. In some cases polarity is discussed further in the section on characters used in analysis (p. 216).

Conflict of evidence

In most characters, the evidence for polarity is unequivocal, although its strength varies considerably. However, there are twelve in which there is some conflict between the sources of polarity evidence: 1, 7, 11, 22, 26, 28, 31, 32, 41, 43, 61 and 66. In character 1, ontogeny conflicts with a wide range of other evidence and can be discounted. In most of the others, outgroup evidence contradicts that from other sources, but in general the former is relatively weak, the presumed primitive state being found in the majority of other scincomorphs, rather than being the only condition in outgroups. Consequently, it seems appropriate to accept the evidence from other sources, at least initially. In characters 22, 28, 31, 32 and 43, outgroup evidence is generally stronger but again is

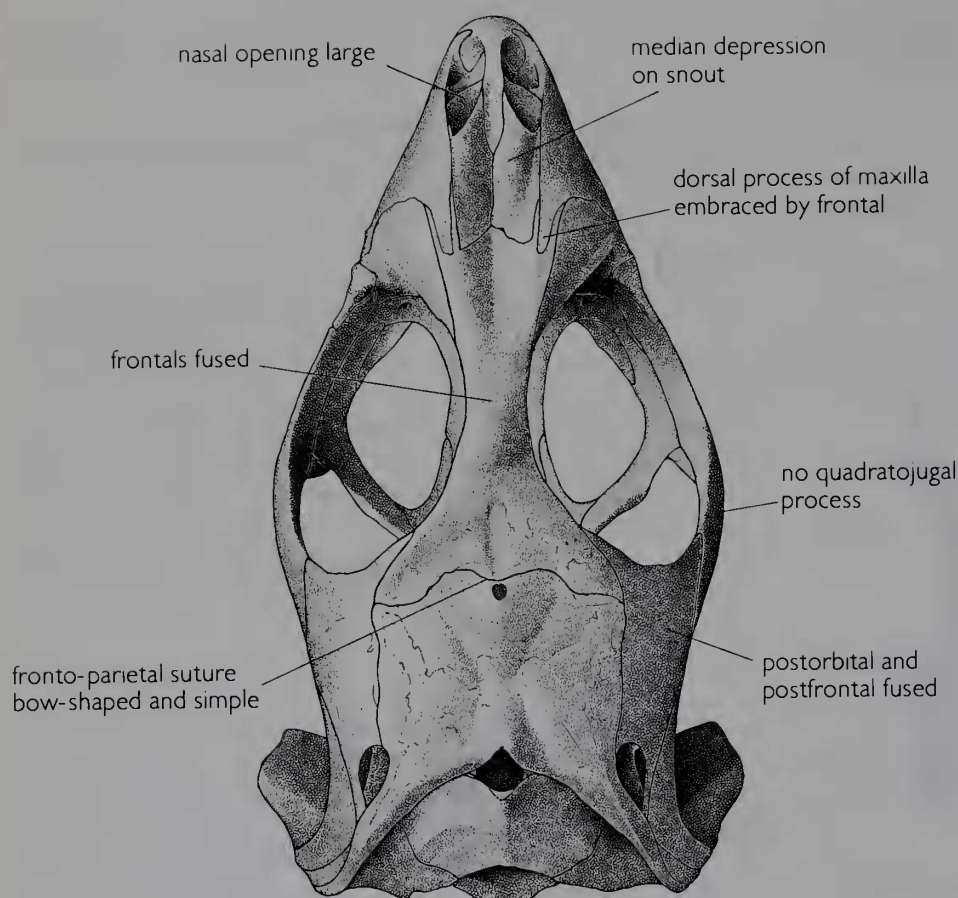


Fig. 3 Skull of advanced lacertid (*Pedioplanis lineoocellata*), with thin osteodermal layer (crusta calcarea), showing common derived conditions. The cranial osteoderms terminate more anteriorly than in primitive forms.

contradicted by other sources which will be provisionally accepted, although conflict here is more severe. Because of this, the data set is also analysed with these particular polarities reversed (p. 231).

CHARACTERS USED IN ANALYSIS

Characters used in analysis are listed below and their distribution summarised in Appendix 2. Each primary character is numbered. Where these have more than two states they are divided into further binary characters, which are designated by figures after a decimal point. Each state of a binary character is indicated by 0 or 1, the former being attached to the apparent primitive condition of the character. Eighty-four primary characters are used, producing a total of 112 binary characters. Borders between some character states are of necessity rather arbitrary. References to fuller explanations of some characters are given, and hemipenial features are described elsewhere (Arnold, 1986a, 1973).

Skull

1 *Nasal opening of skull* (Figs 2,3). Small (0); large (1).
2.1, 2.2, 2.3, 2.4 *Septomaxilla* (Fig.4). Simply convex above with a rounded posterior margin and a narrow anterior shelf with at most slight anterior and posterior projections (0,0,0,0) – Fig. 4a; with distinct and widely separated

anterior and posterior projections (1,0,0,0) – Fig. 4b; with distinct and widely separated anterior and posterior projections and a clear posterolateral process (1,1,0,0) – Fig. 4c; with distinct posterior projection and posterolateral process but no anterior projection (1,1,1,0) – Fig. 4d; with distinct posterior projection and posterolateral process, no anterior projection but an anterolateral process (1,1,1,1) – Fig. 4e, f.

3.1, 3.2 *Medial depression on snout* (Figs 2,3). Absent (0,0); weak (1,0); strong (1,1).

4 *Frontal bones* (Figs 2,3). Separate throughout life (0); fused, at least in mature animals (1).

5 *Dorsal process of maxilla* (Figs 2,3) Broad, at most only slightly embraced by processes of frontal bone (0); narrower and often quite extensively embraced by narrow processes of frontal bone (1).

6.1, 6.2 *Anterior descending processes of frontal bone*. Reaching palatines and in continuous contact with prefrontal, so anterior surface of orbit is completely bony (0,0); not descending fully or a window present between each process and the adjoining prefrontal bone (1,0); processes absent (1,1).

7 *Fronto-parietal suture* (Figs 2,3). Convex anteriorly, the median section interdigitating strongly with the frontal (0); typically bow-shaped with a small concavity near midline, only quite weakly interdigitating with the frontal or scarcely at all (1).

8 *Length of parietal bone/length of section bearing osteoderms or at least covered by large dermal plates*. Less than 1.45 (0); more than 1.45 (1).

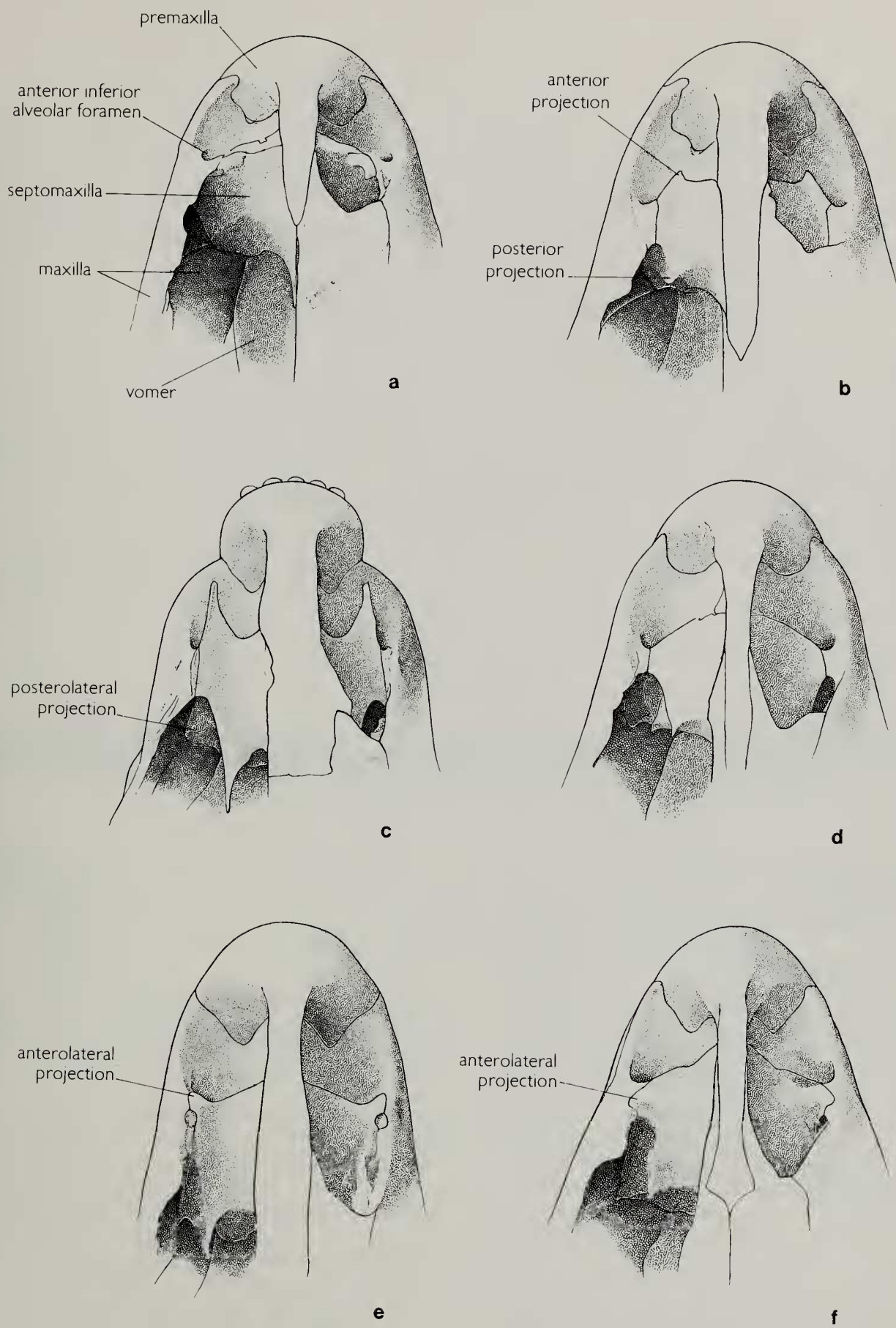


Fig. 4 Snouts of lacertid skulls with the left nasal cavity opened to show variation in the septomaxilla. a. '*Lacerta*' *jacksoni*'; b. *Gallotia atlantica*; c. *Acanthodactylus schmidtii*; d. *Pedioplanis laticeps*; e. *Mesalina balfouri*; f. *Ophisops elegans*.

9 Width of parietal bone/length of section bearing osteoderms or at least covered by large dermal plates. Less than 1.05 (0); more than 1.05 (1).
10.1, 10.2. Pineal fontanelle (Figs 2,3). Present (0,0); absent in many but not all individuals, or reduced (1,0); absent in all cases (1,1).

11 Cranial osteoderms (Figs 2,3). Reaching the back of the parietal bone extensively in medial area (0); not extending this far posteriorly or only over a small area (1).
12 Postfrontal and postorbital bones (Figs 2,3). Separate in adults, with rare exceptions (0); fused in adults and most young animals (1).

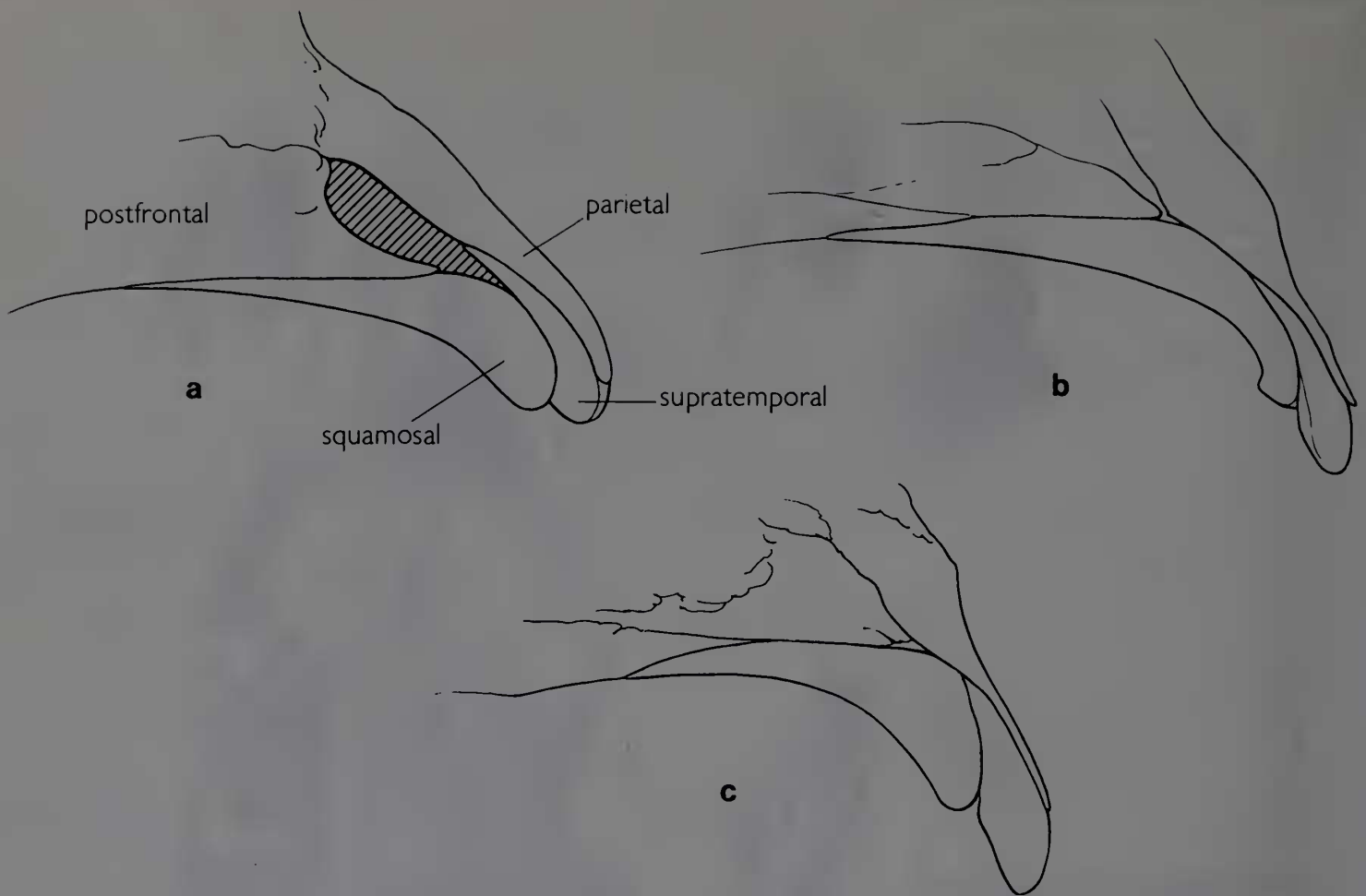


Fig. 5 Posterolateral aspects of lacertid skulls (anterior to left), showing variation in shape of squamosal bone and its relationship to the supratemporal process of the parietal bone. a. fairly slender, separated from parietal (*Eremias arguta*); b. slender, in contact with parietal (*Nucras taeniolata*); c. deep posteriorly, in contact with parietal (*Pedioplanis lineoocellata*).

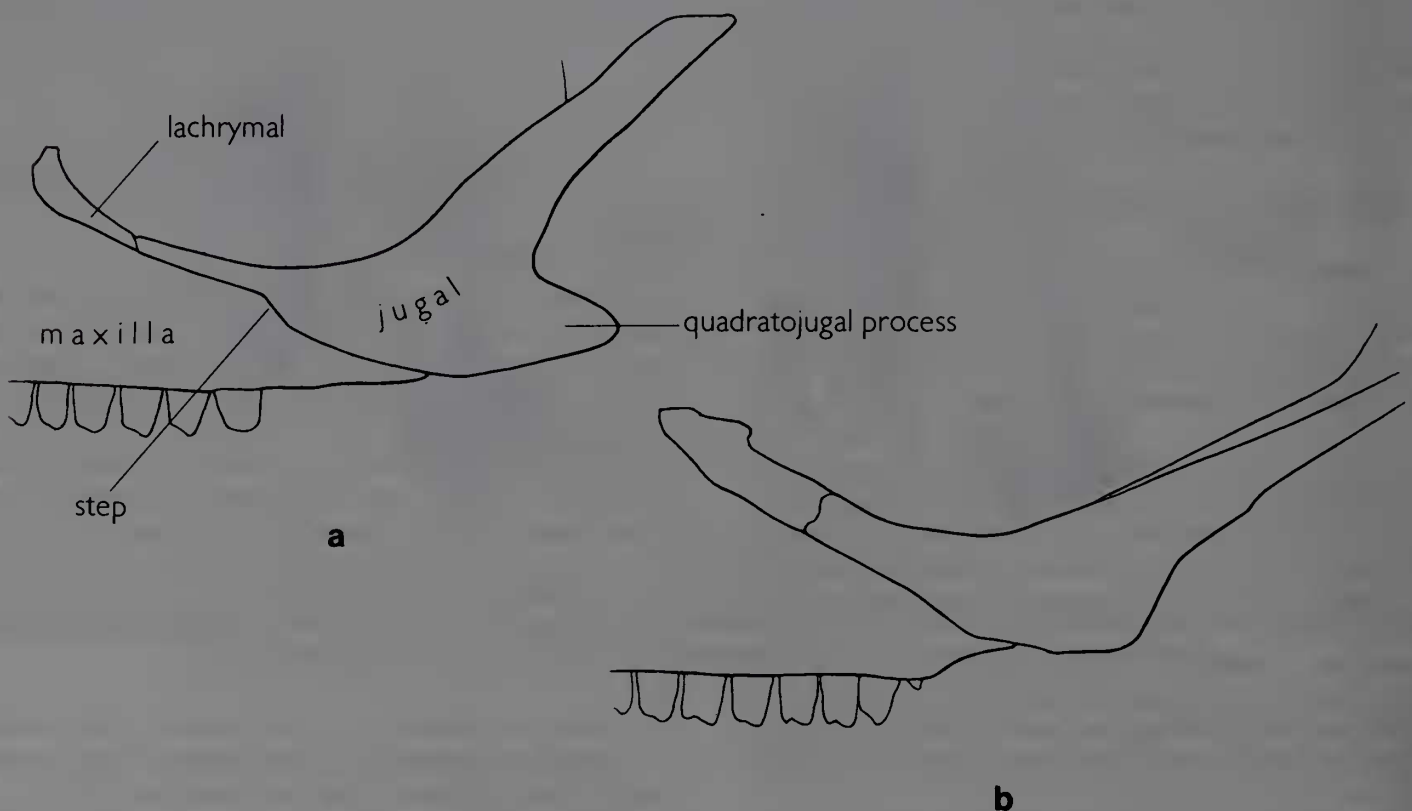


Fig. 6 Suborbital area of lacertid skulls in lateral view, showing presence or absence of quadratojugal process on jugal bone, variation in extent of anterior jugal exposure, and presence or absence of a 'step' in the lower border of the jugal.

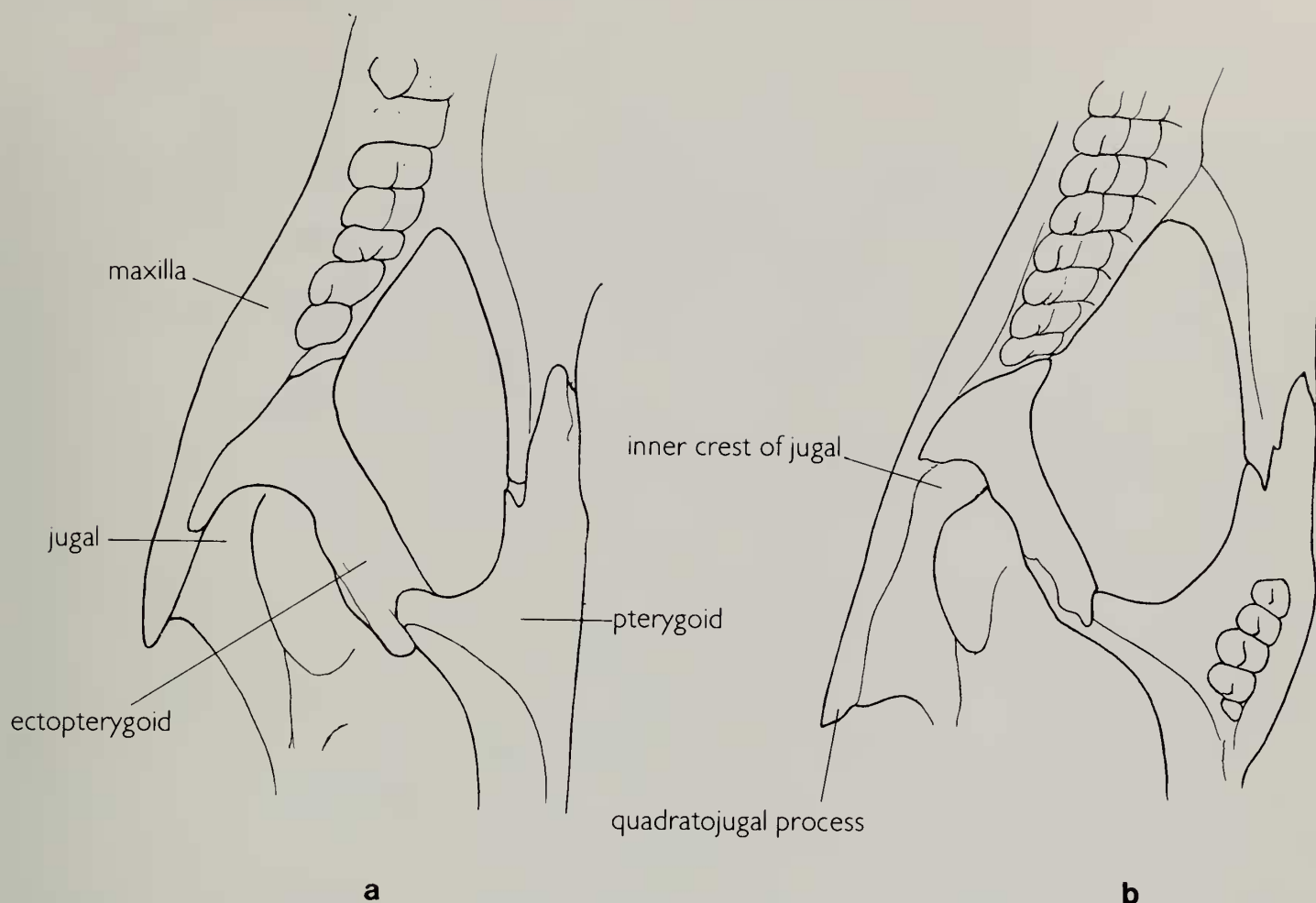


Fig. 7 Right suborbital region of lacertid skulls in ventral view. a. *Podarcis sicula*; b. *Psammodromus algirus* with inner crest of jugal bone clearly visible behind ectopterygoid.

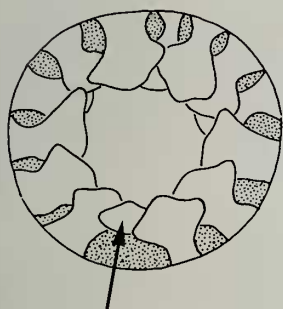


Fig. 8 Scleral ossicles of *Acanthodactylus*; arrow indicates scleral ossicle 14 which lacks a peripheral radial portion. From Arnold (1983).

Post-cranial skeleton

22.1, 22.2 *Clavicle* (Fig. 9). Variable within species, medial part loop-shaped, either continuous or interrupted posteriorly (0,0); always interrupted posteriorly (1,0); never interrupted posteriorly (0,1).

23 *Expansion of medial section of clavicle* (Fig. 9). Strong (0); weak (1).

24 *Shape of interclavicle* (Fig. 10). Cruciform, with arms directed laterally, or obliquely forwards (0); arms directed obliquely backwards (1).

25 *Interclavicle flanged*. No (0); yes (1).

26.1, 26.2, 26.3 *Sternal fontanelle* (Fig. 10). Large and roughly elliptical (0,0,0); sometimes very weakly heart-shaped (1,0,0); clearly heart-shaped in at least some individuals (1,1,0); small and round, or absent (0,0,1).

27 *Xiphisternal cartilages* (Fig. 10). Close together or in contact (0); well separated (1).

28 *Marked sexual variation in number of presacral vertebrae*. Yes (0); no (1).

Outgroup analysis among the Scincomorpha suggests that marked sexual variation is likely to be the derived condition in lacertids. But the alternative state (little or no sexual variation) has a very restricted distribution in the Lacertidae. It occurs in a few species of *Acanthodactylus*, where outgroup comparison within Ethiopian and advanced Saharo-Eurasian genera indicates it is secondary, and also in *Gallotia*, where outgroup comparison among related primitive forms suggests the same thing.

13 *Contact between squamosal and parietal bones* (Fig. 5). Absent (0); present (1).

14 *Shape of squamosal bone* (Fig. 5). Slender (0); deep posteriorly (pistol shaped) (1).

15 *Quadratojugal process on jugal bone* (Fig. 6). Distinct (0); usually very reduced or absent (1).

16 *Exposure of anterior part of jugal bone on side of skull* (Fig. 6). Small (0); large (1).

17 *Lower border of outer face of jugal bone* (Fig. 6). Not markedly stepped (0); often markedly stepped (1).

18 *Inner crest of jugal bone clearly visible behind ectopterygoid in ventral view* (Fig. 7). No (0); yes (1).

19 *Ossification of temporal scales*. Not extensive (0); extensive (1).

20 *Lateral teeth*. With two cusps or sometimes one (0); usually with three or more cusps (1).

21 *Peripheral radial portion of scleral ossicle 14* (Fig. 8). Present (0); absent (1).

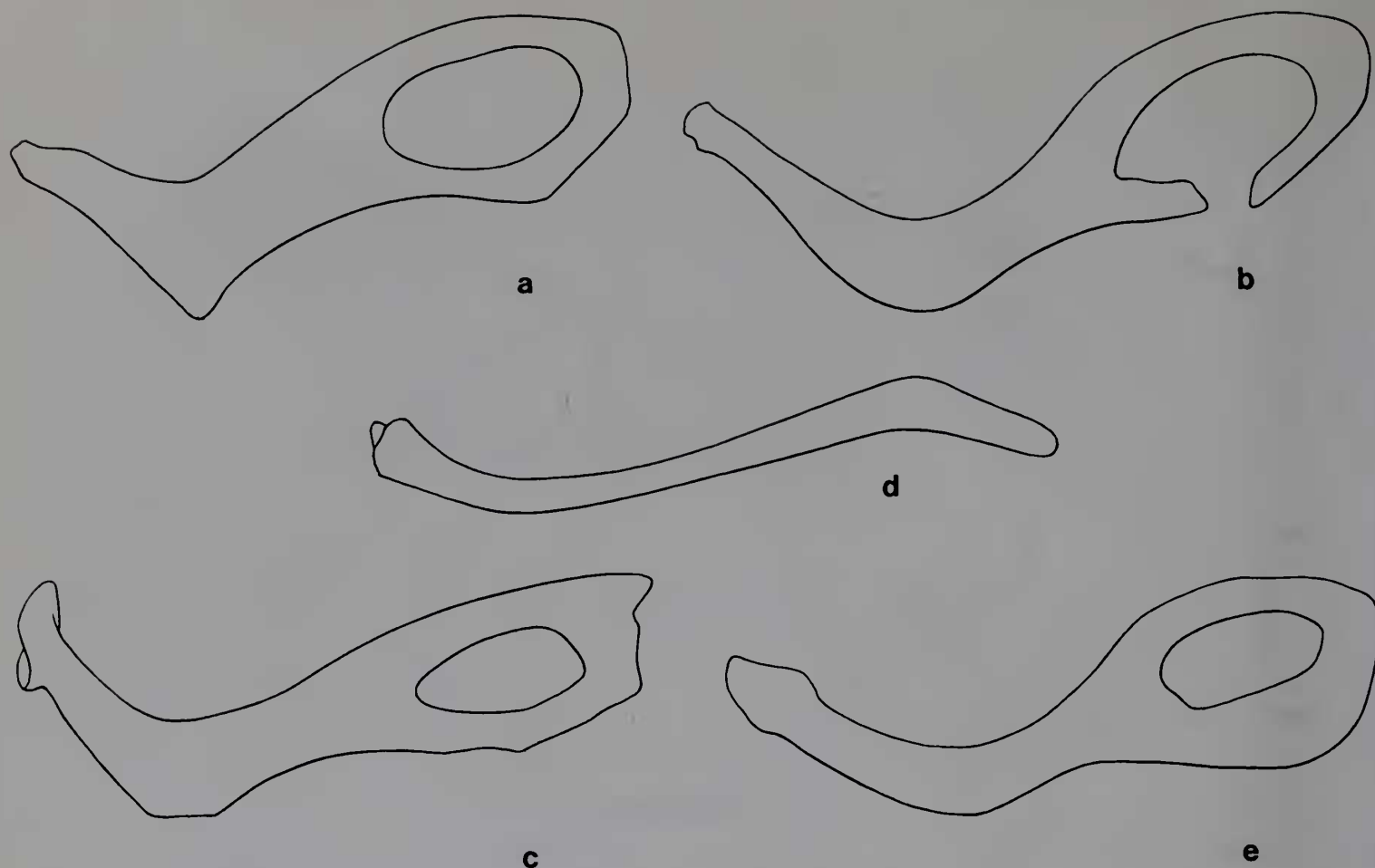


Fig. 9 Right clavicles in ventral view, showing variation in medial area. a. strongly expanded, forming continuous loop (*Lacerta* s. str.); b. strongly expanded, loop interrupted posteriorly (*Lacerta* s. str.); c. weakly expanded, forming continuous loop ('*Lacerta*' *echinata*); d. posterior section completely absent (*Holaspis guentheri*); e. weakly expanded, forming continuous loop with posterior border thickened (*Adolfus vauereselli*).

29 *Number of short free dorsal ribs*. Equal or less than number of long free dorsal ribs (0); More than number of long free dorsal ribs (1).

30 *Inscriptional ribs*. Often present (0); often absent (1).

31.1, 31.2, 31.3 *Transverse processes on anterior automatic caudal vertebrae* (Fig. 11). Variable within species, in some individuals a long anterior pair of processes more or less at right angles to the vertebra and a shorter parallel posterior pair—pattern B, others lack the posterior pair—pattern A (0,0,0); only anterior pair present in all individuals—pattern A (1,0,0); a long anterior pair and a posterior pair that diverges posteriorly and may sometimes be rather longer—pattern BC (0,1,0); posterior pair diverging posteriorly and always longer than anterior one—pattern C (0,1,1).

Etheridge (1967) considered pattern C as the primitive one in lacertids, but it and pattern A are both widespread in lizards as a whole and, if anything, the assumption that pattern A is derived is more parsimonious overall. Among advanced lacertids, the distribution of other characters in compatibility analysis suggests that the C pattern in *Acanthodactylus*, *Mesalina* and *Ophisops-Cabrera* arose directly or indirectly from pattern A (p. 230). An indication that such a change is possible is provided by a specimen of *Pedioplanis lineocellata* (BMNH 98.5.4.3) in which one side of the tail shows the A pattern, like other members of *Pedioplanis*, while the other exhibits a close approximation to the C condition. Distribution of other characters also indicates that the C pattern is likely to be derived from the BC pattern in *Psammmodromus* and *Gallotia* (p. 232) and from the A/B polymorphism in

Podarcis (p. 234). Compatibility analysis associating *Lacerta jayakari* with Ethiopian and advanced Saharan and Eurasian lacertids, and commonality within primitive lacertids both suggest that the A/B polymorphism is likely to be primitive.

External features of head (Fig. 12)

32 *Postnasal scales*. Two superposed (0); single (1).

33 *Contact between postnasal and supranasal scales below level of nostril*. Absent (0); present (1).

34 *Lower postnasal scale extending anteriorly to contact rostral scale* (Fig. 13). No (0); yes (1).

35 *Contact between supranasal and anterior loreal above single postnasal*. Absent (0); present (1).

36 *Extended lower postnasal divided*. No (0); yes (1).

37 *Width of rostral scale*. Normal (0); narrow with sides sloping inwards towards mid-line (1).

38 *Second supraciliary scale elongate, extending posterior to suture between second and third supraoculars*. No (0); yes (1).

39.1, 39.2 *Position of lateral border of parietal scale relative to parietal table of skull* (Fig. 14). Not reaching edge of table (0,0); reaching edge of table posteriorly (1,0); reaching edge of table anteriorly as well (1,1).

40.1, 40.2 *Size of occipital scale*. Normal (0,0); broad, as wide as posterior border of frontal in adults (1,0); strongly reduced or absent (0,1).

41.1, 41.2 *Interparietal scale*. Normal (0,0); often enlarged (1,0); absent or extremely reduced (0,1).

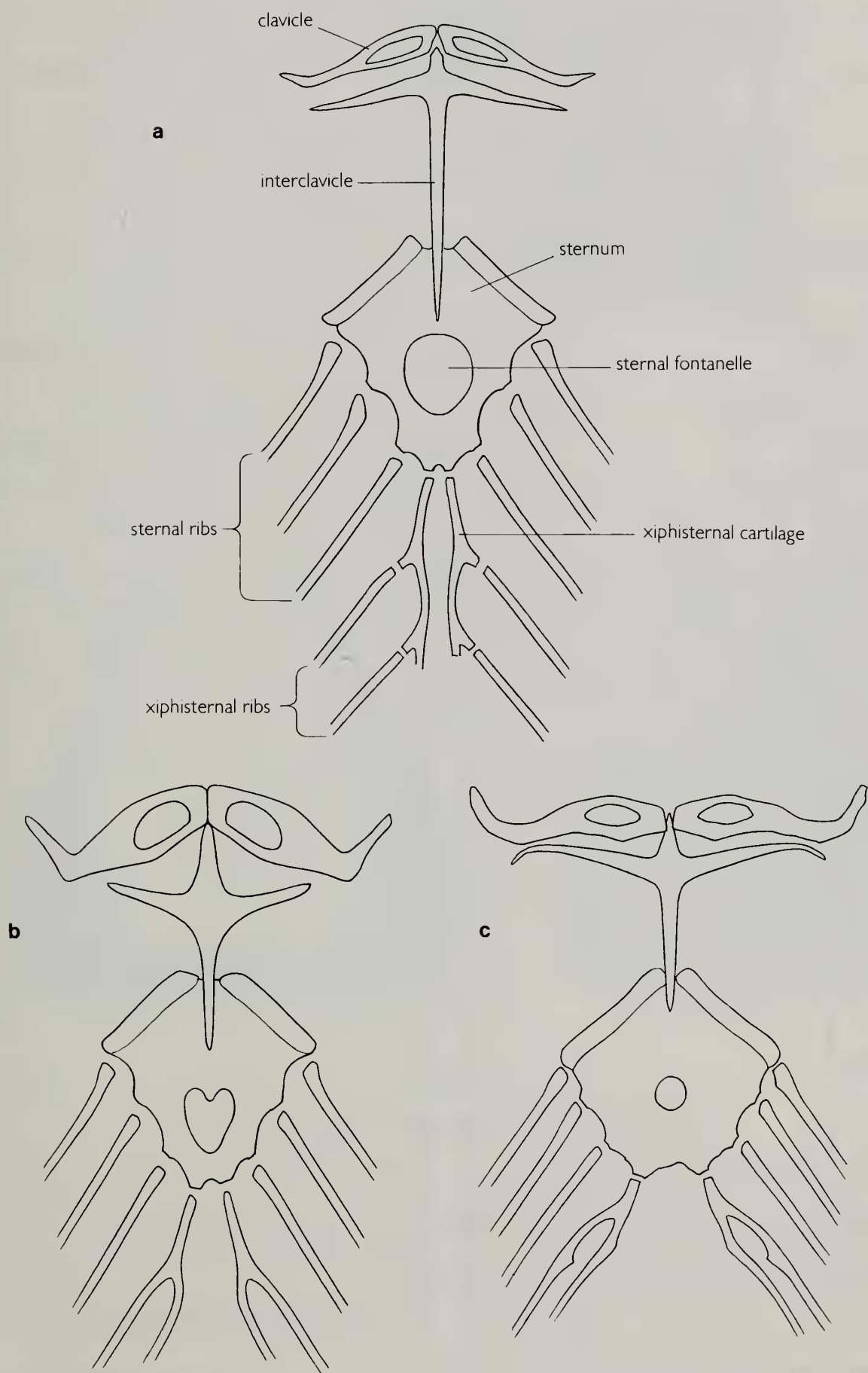


Fig. 10 Clavicles, interclavicles, sterna and associated ribs and cartilages, showing variation. a. Interclavicle with arms directed obliquely backwards, sternal fontanelle large and elliptical, xiphisternal cartilages close together (*Lacerta dugesii*); b. interclavicle with arms directed obliquely forwards, sternal fontanelle heart-shaped, xiphisternal cartilages distinctly separated (*Acanthodactylus boskianus*); c. interclavicle with arms directed obliquely forwards, sternal fontanelle small and round, xiphisternal cartilages broadly separated (*Meroles ctenodactylus*).

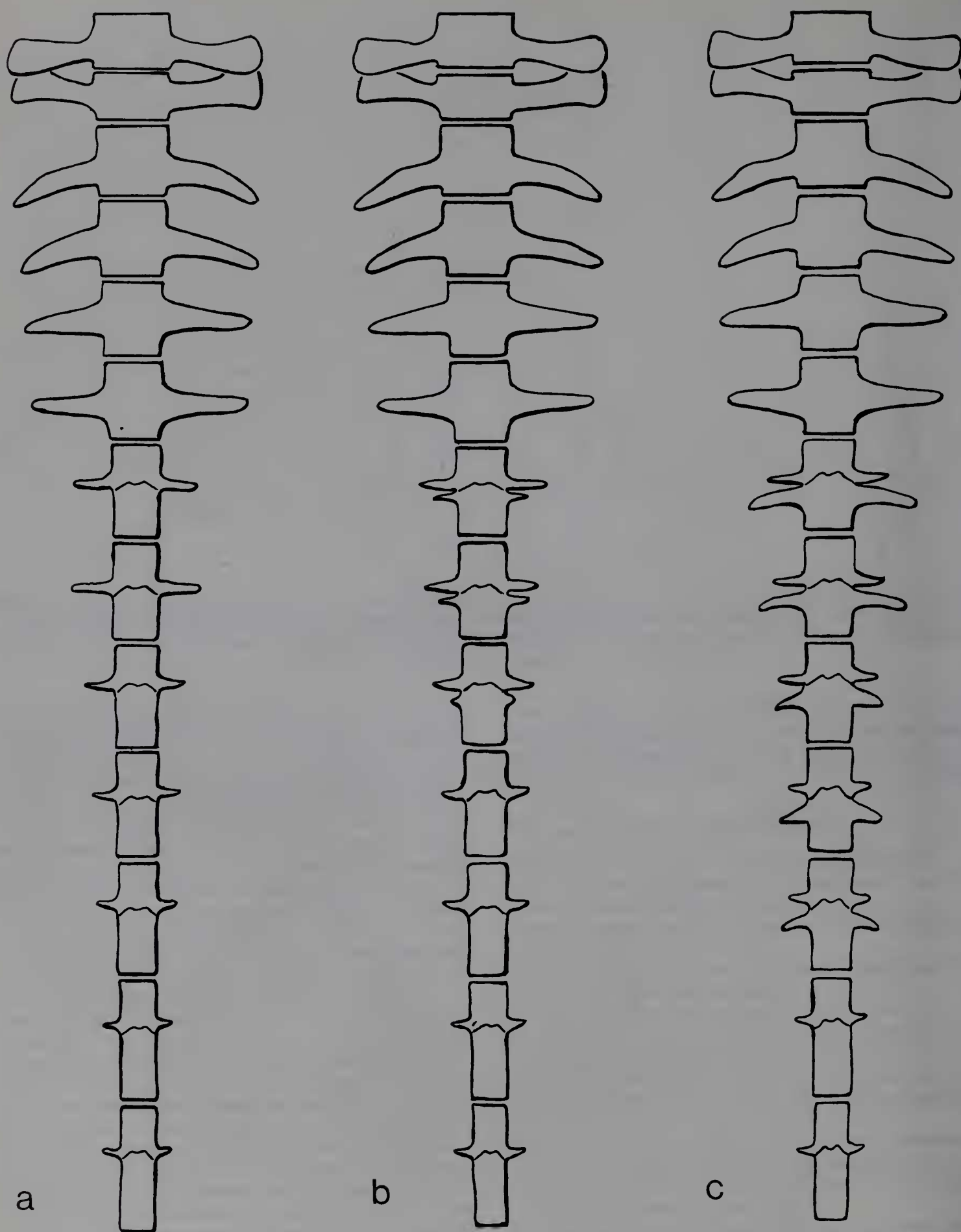


Fig. 11 Caudal vertebrae, showing principal variations in transverse processes of anterior autotomic vertebrae. a. Pattern A—a single anterior pair of processes; b. Pattern B—an anterior pair of processes followed by a parallel shorter pair; c. Pattern C—an anterior pair of processes followed by a longer posterior pair that diverge backwards. The BC pattern is intermediate between B and C: the posterior processes diverge posteriorly but are not always longer than the anterior ones. From Arnold (1973).

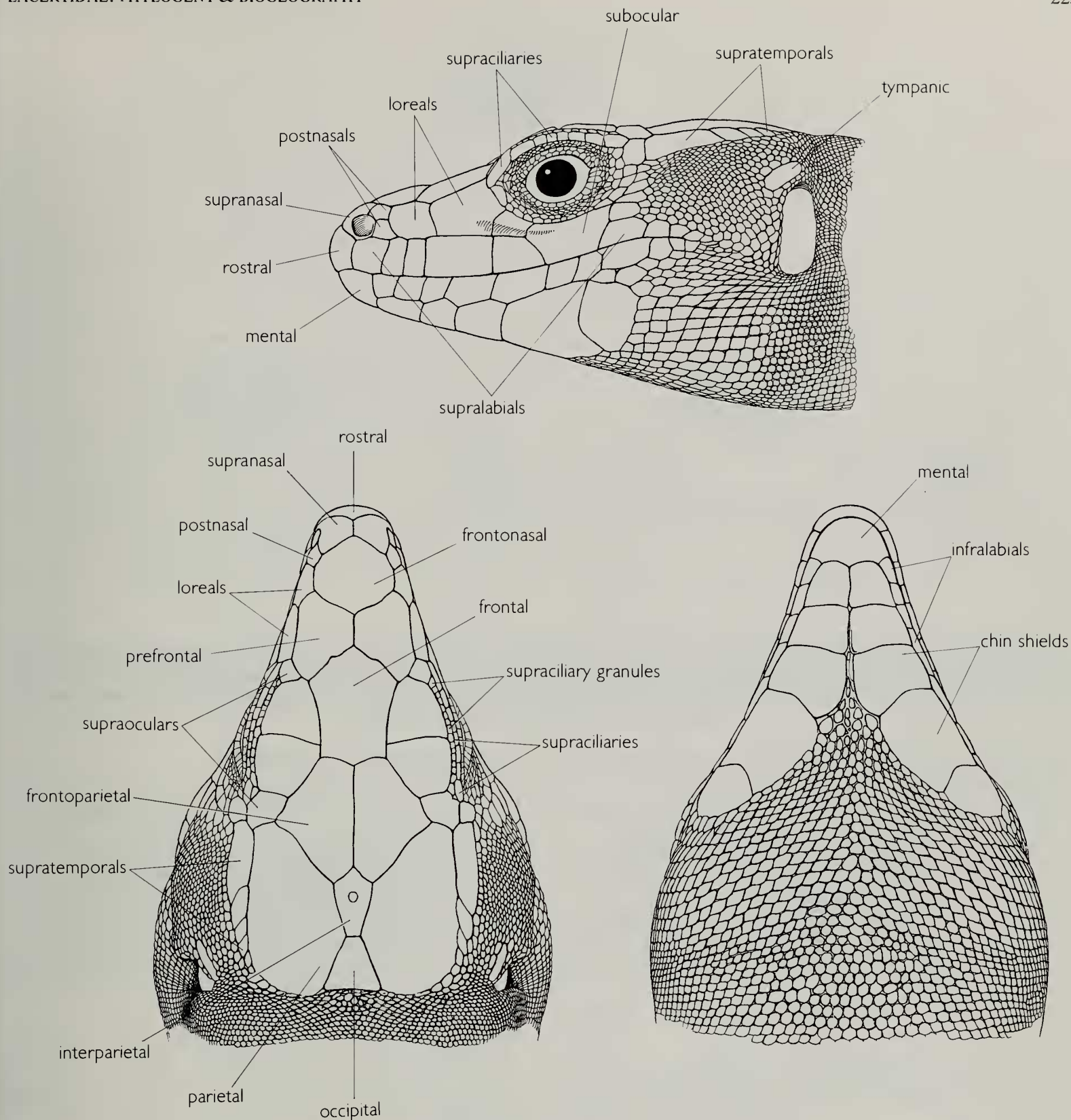


Fig. 12 Head scaling of *Lacerta jayakari*. From Arnold (1986d).

42 *Transparent 'window' in lower eye-lid* (Fig. 15). Absent (0); present (1).

43 *Masseteric scale* (an isolated large scale in temporal region). Present in at least some individuals (0); always absent (1).

44 *Chin shields*. Five or more pairs contacting the infralabials on each side (0); four pairs contacting the infralabials (1).

External features of body, limbs and tail

45.1, 45.2, 45.3 *Collar beneath throat* (a posteriorly directed transverse fold covered externally by large scales). Well developed with granules beneath (0,0,0); well developed,

but no granules beneath and fixed at centre (1,0,0); weak (1,1,0); absent (1,1,1).

46 *Mid-dorsal body scales*. Small (0); large (1)

47 *Lateral body scales*. Small (0); large (1).

48.1, 48.2 *Number of longitudinal rows of ventral body scales*.

Usually six (0,0); usually eight (1,0); usually ten or more (0,1).

In lacertids with large dorsal scales, it is often difficult to decide where these end and the equally large ventrals begin. But in forms with small dorsal scaling easily distinguished from the ventrals, the lateral margin of the latter corresponds closely to that of the rectus abdominis lateralis muscle. In species with large dorsal scales, this muscle will consequently

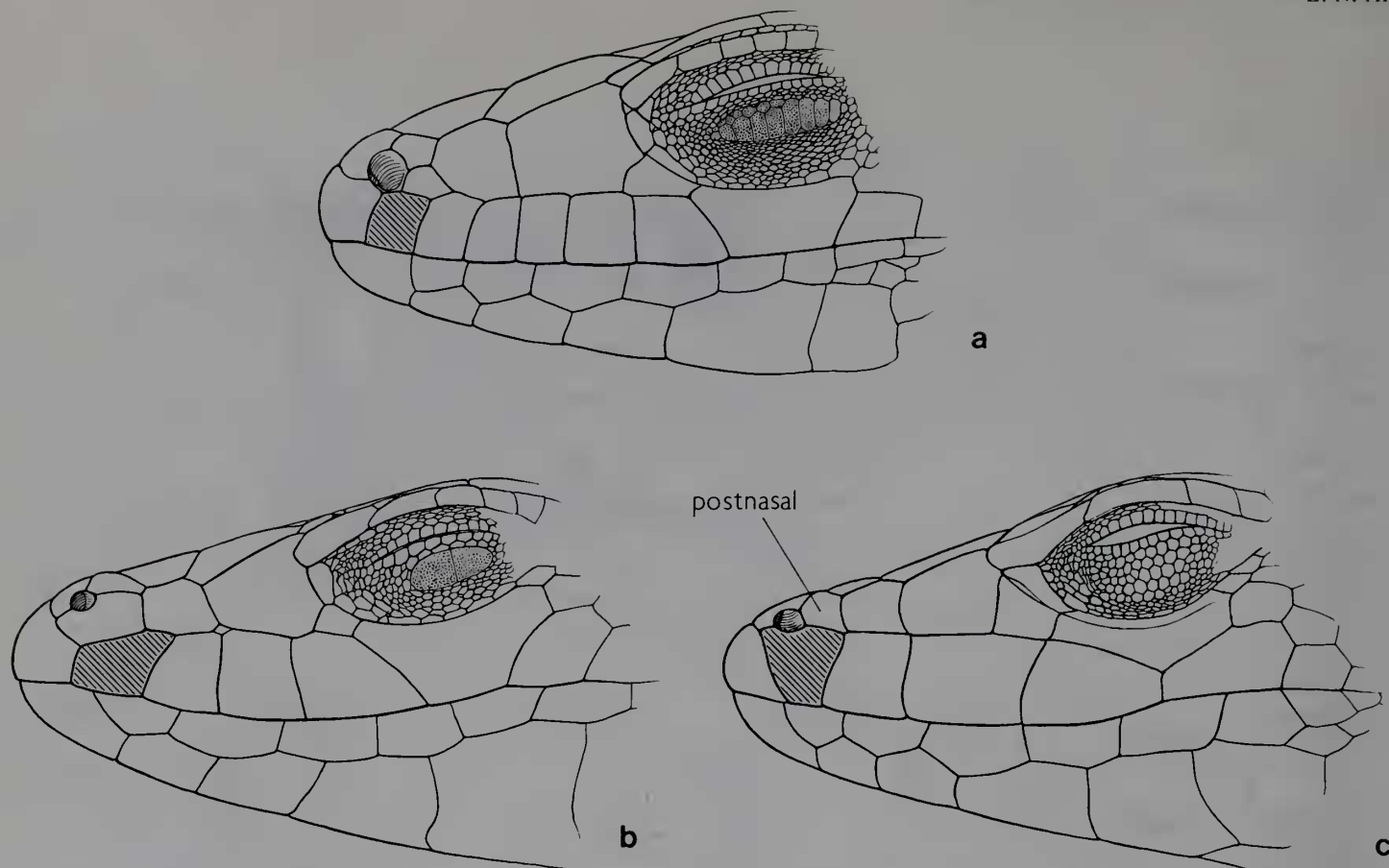


Fig. 13 Snouts of lacertid lizards, showing some variations in nasal scaling. a. First upper labial scale contacts nostril; two postnasals (*Lacerta jayakari*). b. First upper labial scale separated from nostril; two postnasals, the lower extending anteriorly to contact rostral scale (*Mesalina adramitana*). c. First upper labial scale, which has its sides converging downwards, in contact with nostril; a single postnasal (*Acanthodactylus boskianus*). First upper labial scale shaded in all cases.

be used to define the ventrals in which any scale at least partly overlying it will be included.

49.1, 49.2 *Keeling on ventral body scales*. None (0,0); outer row on each side keeled (1,0); all rows keeled (1,1).

50 *Arrangement of ventral body scales*. In more or less straight longitudinal rows (0); tessellated, so that rows tend to run diagonally (1).

51.1, 51.2 *Row of femoral pores*. Running at least two-thirds of the distance from mid-line to knee (0,0); reduced, but more than half this distance (1,0); reduced to 1–5 pores in inguinal area (0,1).

52 *Shape of scales bearing femoral pores* (Arnold, 1989, Fig. 4). Flattish (0); tuberculate (1).

53.1, 53.2 *Lateral scale rows on fingers* (Fig. 16). None (0,0); a posterior lateral row present (1,0); a posterior and an anterior row present (1,1).

54.1, 54.2 *Lateral scale rows on toes* (Fig. 16). None (0,0); a posterior lateral row present (1,0); a posterior and an anterior row present (1,1).

55 *Subdigital lamellae*. Smooth or tuberculate (0); keeled (1).

56 *Axillary mite pocket* (Arnold, 1986c). Absent (0); present (1).

57 *Post-femoral mite pocket* (Arnold, 1986c). Absent (0); present (1).

58 *Scales bordering ventral mid-line of tail*. Narrow, not much wider than adjoining scales (0); broad, much wider than adjoining scales (1).

59 *Micro-ornamentation on dorsal body scales*. Not coarsely striate (0); coarsely striate (1).

60 *Blue pigment on outer ventral scales*. Present (0); absent (1).

Various soft-part characters

61 *Tongue colour*. Predominantly dark (0); predominantly light (1).

62.1, 62.2 *Post-nasal area* (Fig. 17). Thin in horizontal section (0,0); somewhat thickened (1,0); very thick (1,1).

63.1, 63.2, 63.3, 63.4 *Nasal vestibule* (Fig. 17). Short (0,0,0,0); some elongation (1,0,0,0); vestibule overhangs posteriorly (1,1,0,0); septomaxilla largely covered by vestibular overhang (1,1,1,0); vestibular overhang covers anterior part of concha where it attaches to lateral wall of nasal cavity (1,1,1,1).

64 *Anterior extent of kidney*. Less than half length of kidney in front of sacrum (0); more than half in front of sacrum, anterior section usually expanded (1).

65 *Posterior extent of kidney*. Extends well posterior to level of vent (0); barely reaches level of vent or not at all (1).

66 *Insertion of m. retractor lateralis anterior in front of vent* (Arnold, 1984). Near mid-line (0); more laterally (1).

67 *Size of m. retractor lateralis anterior in front of vent* (Arnold, 1984). Narrow, with no fibres extending to region of vent lip (0); broad with some fibres extending posteriorly to region of vent lip (1).

68 *Some fibres of m. retractor lateralis anterior reaching base of hemipenis* (Arnold, 1984). No (0); yes (1).

69.1, 69.2 *Thoracic fascia*. None (0,0); lateral (1,0); extending to mid-line (1,1).

This structure is a superficial fascia lying just beneath the skin that overlies the thoracic region. When the fascia is present, the anterior of the m. rectus abdominis lateralis attaches to it. The fascia terminates anteriorly in the region of the lateral

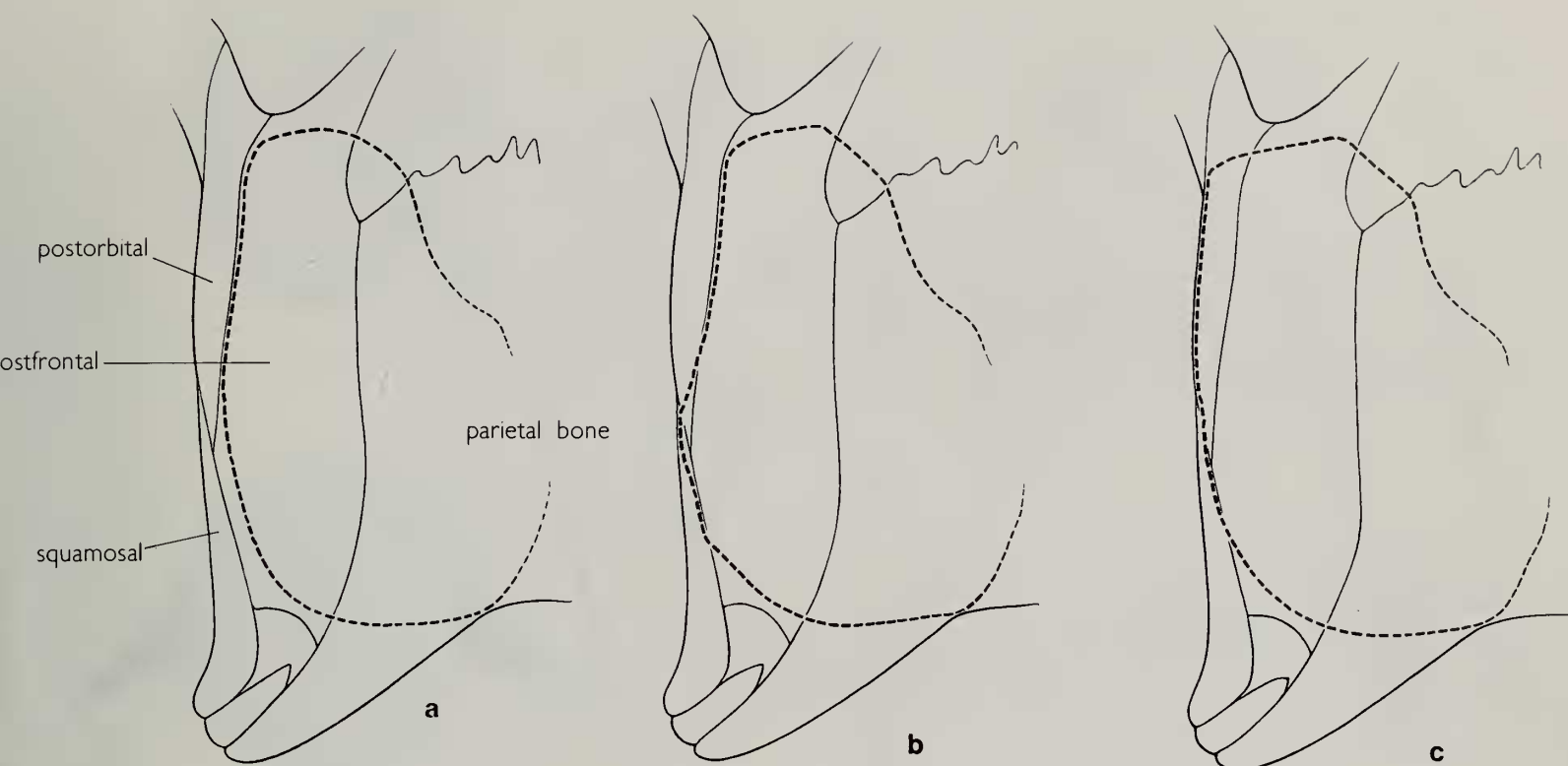


Fig. 14 Relationship between the outer margin of the left parietal scale (indicated by broken line) and the underlying bones of the skull. a. Parietal scale margin not approaching edge of parietal table; b. Parietal scale margin approaching edge of table posteriorly (on squamosal bone); c. Parietal scale margin approaching edge of parietal table posteriorly and anteriorly (on squamosal and postorbital bones).

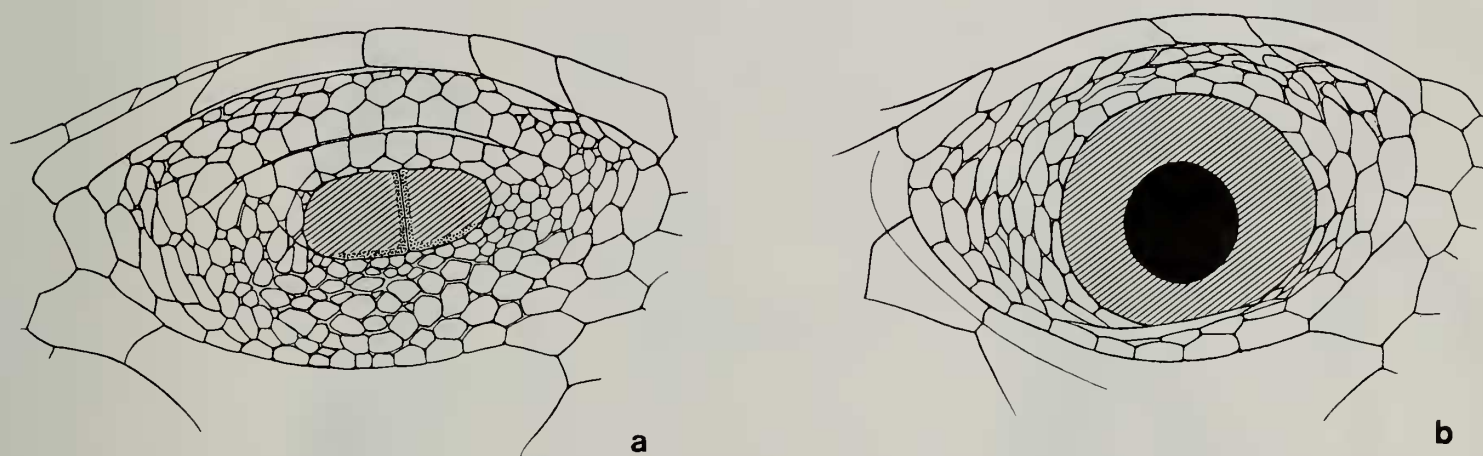


Fig. 15 Closed eyelids of left eyes, showing development of transparent 'windows'. a. Moderate, composed of two scales (*Mesalina guttulata*); b. huge, composed of a single scale, the eyelids fused (*Ophisops elbaensis*)

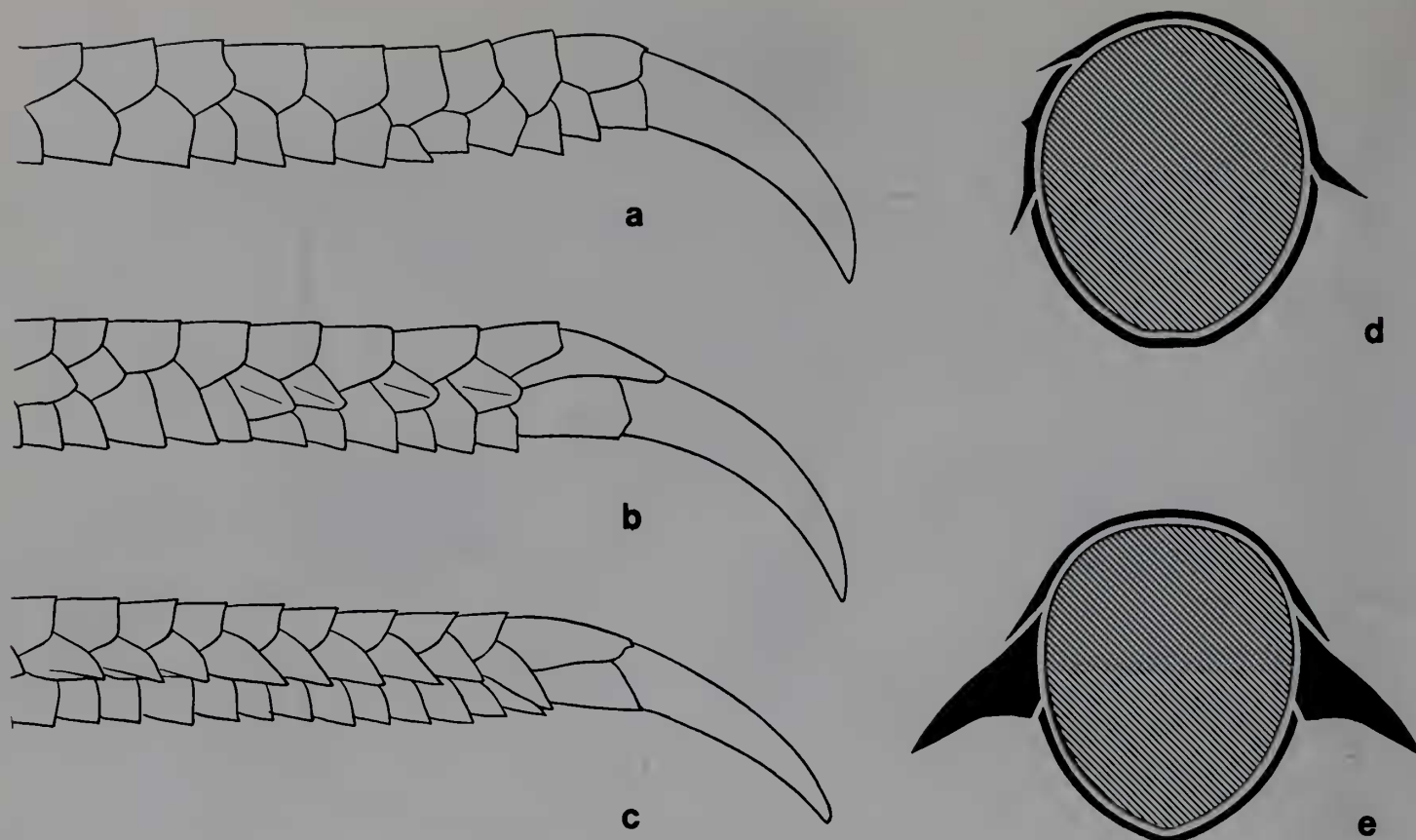


Fig. 16 Scaling on digits. a. No lateral scale row present. b, c. Partial and complete lateral row present. d. Transverse section of digit with a posterior lateral row. e. Transverse section of digit with posterior and anterior lateral rows. From Arnold (1986d).

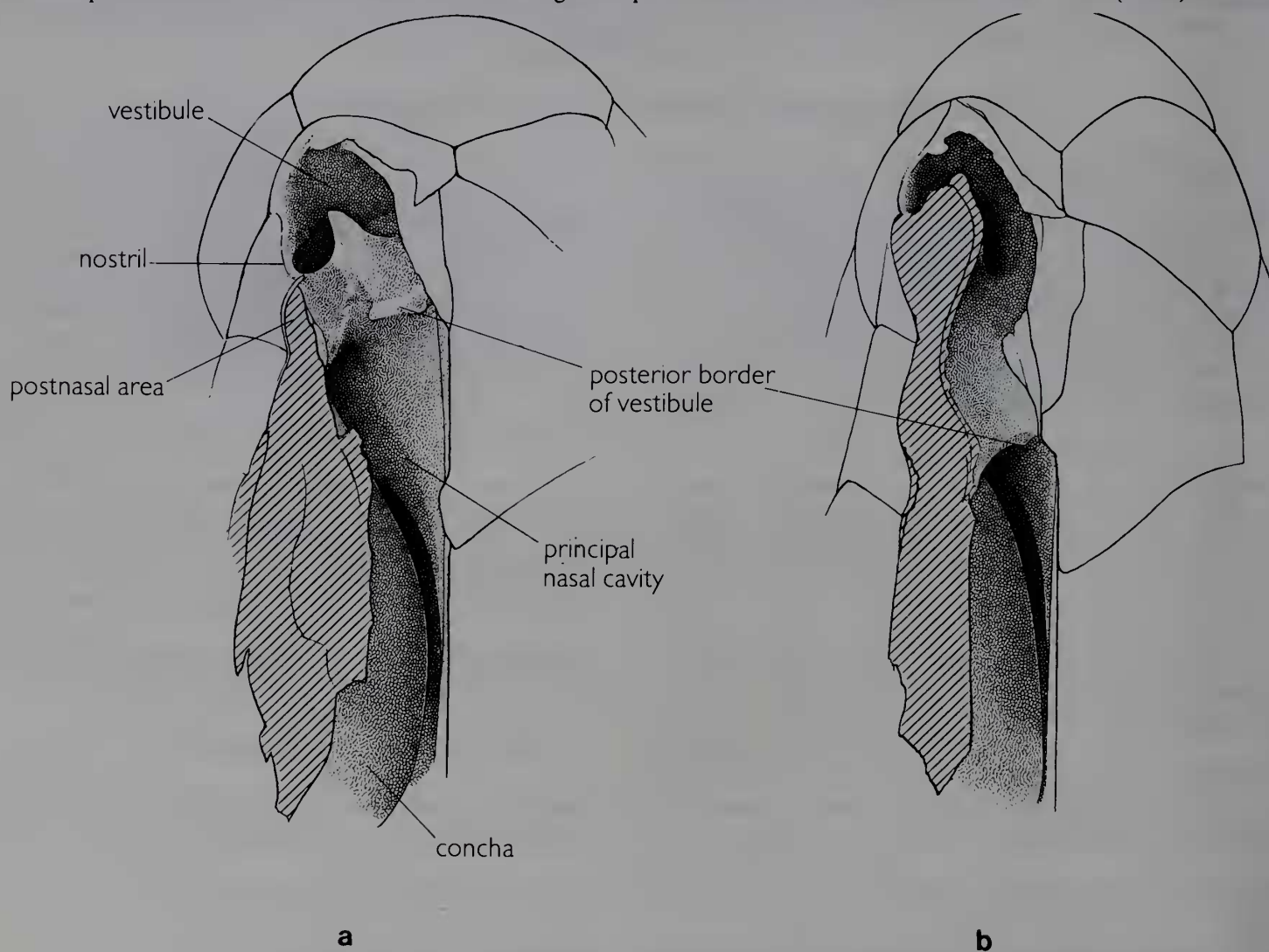


Fig. 17 Snouts of lacertid lizards with left nasal cavity opened to show variation in thickness of postnasal region and length of nasal vestibule. a. '*Lacerta*' *jacksoni*; b. *Acanthodactylus cantoris*. Cut areas are hatched.

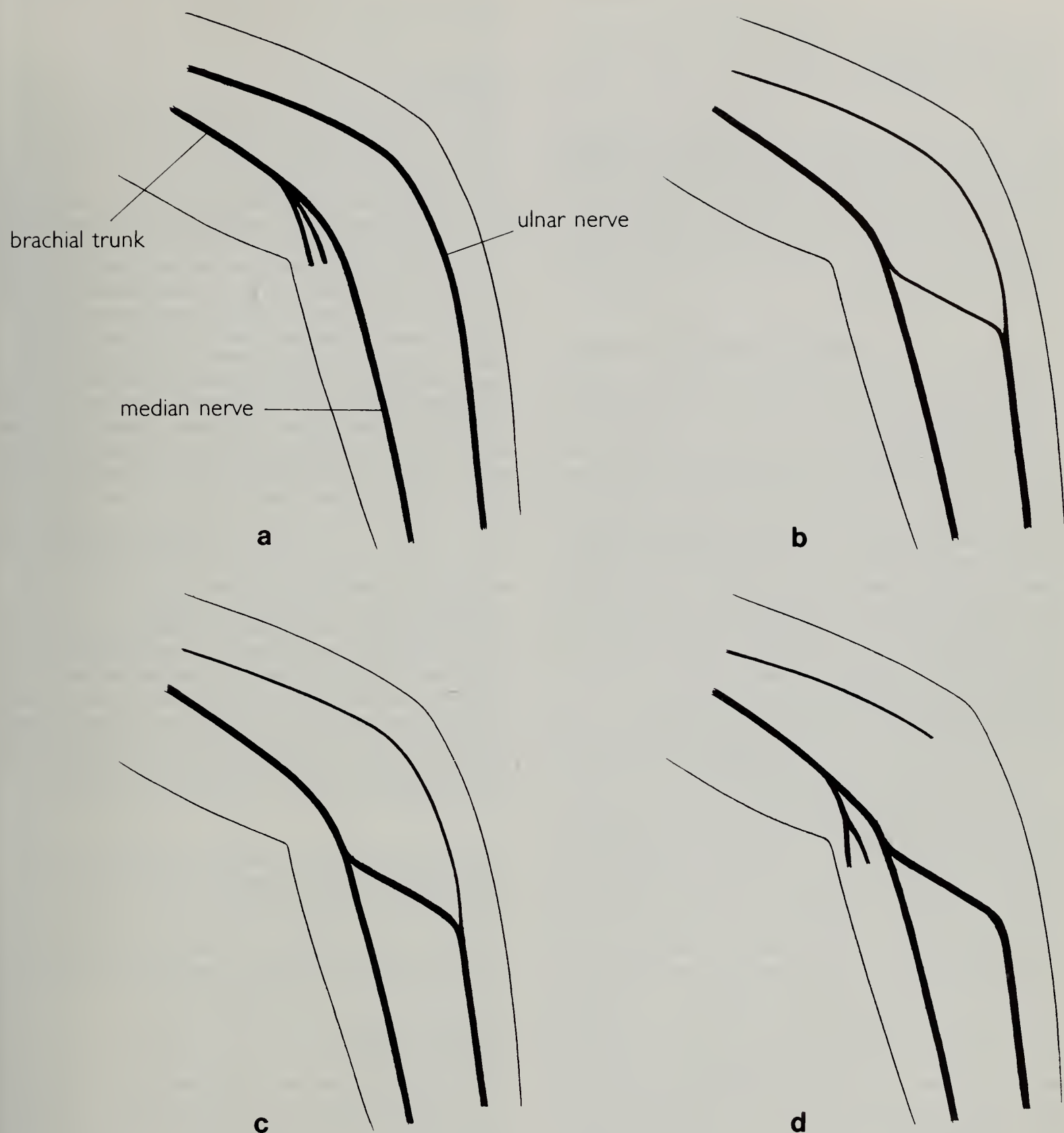


Fig. 18 Ulnar nerve patterns in lacertid lizards. a. 'Lacertide' pattern found in primitive Eurasian species. b. Intermediate pattern of '*Lacerta*' *jacksoni* and *Adolfus allenii*. c. Intermediate pattern of '*Lacerta*' *echinata* and some *Adolfus africanus*. d. 'Varanide' pattern of advanced lacertids.

arms of the interclavicle. It is frequently absent (0,0) and may be partial so that it does not cover the median area of the thorax (1,0). At its greatest extent, it reaches the midline over a considerable area of the anterior thorax (1,1).

70 Hemipenial armature. Absent (0); present (1).

There is evidence that absence of an armature, or its presence in only restricted form, may be a secondary condition, even

though overall out-group comparison suggests that absence is the primitive state (Arnold, 1986a). This appears to be true in some species of *Pedioplanis*, *Meroles*, *Mesalina*, *Acanthodactylus* and *Eremias* in which the armature is not present in its full form. But absence of an armature may indeed be truly primitive in Palaearctic forms assigned to *Lacerta*, *Algyroides*, *Psammodromus*, *Gallotia*, *Podarcis*, *Takydromus* and *Platyplacopus*. A contrary interpretation has been proposed else-

where for the first five of these genera (Arnold, 1986a), but a simpler explanation seems more appropriate.

71 *Cross section of lobes in uneverted hemipenis*. Simple (0); flattened and complexly folded (1).

72 *Length of hemipenial lobes*. Relatively short (0); relatively long (1).

Because this character and the following one are difficult to assess in uneverted hemipenes where the lobes are complexly folded, they have been recorded only in the Palaearctic forms where lobes are nearly always simple and sac-like

73 *Lips on hemipenial lobes*. Moderate or quite small (0); large (1).

74 *Inner connectors arising close to the tips of the hemipenial clavulae*. No (0); yes (1).

75 *Medial side of hemipenis and armature reduced*. No (0); yes (1).

76 *Lateral side of hemipenis and armature reduced*. No (0); yes (1).

77 *Large pointed papillae on hemipenial lobes* (Arnold, 1973). Absent (0); present (1).

78.1, 78.2 *Hemipenial microornamentation*. Crown-shaped tubercles (0,0); bicuspid tubercles (1,0); simple spines (1,1).

Hemipenial sheath. Arnold (1984) noted that most lacertids examined had a membranous sheath around the uneverted hemipenis and associated m. retractor magnus, but that this is missing in *Takydromus*. Investigation of more material makes it apparent that this feature is very variable in its development, so that in some cases it is very difficult to know if it is really present or not. Because of this problem of scoring, it is not included in the analysis presented here.

79 *Female genital sinus*. Bilobed (0); unlobed (1).

80 *Exit of oviducts into genital sinus*. Ventrally, some way from tip(s) of sinus (0); at or near tip(s) or dorsally (1).

81.1, 81.2 *Course of ulnar nerve* (Fig. 18). 'Lacertide' (0,0); intermediate (1,0); 'varanide' (1,1).

Julien & Renous-Lécuru (1972) discuss two patterns of innervation of the lower forelimb in lizards. In the more primitive ('lacertide') condition, the ulnar nerve is completely independent of the brachial trunk and the nerves originating from it, and follows a superficial course in the lower limb (Fig. 18a). In the more advanced ('varanide') condition, there is a common trunk in the upper arm which includes all the fibres of the ulnar nerve that serve the lower limb; these separate only distal to the elbow (Fig. 18d). The authors correctly report both conditions in the Lacertidae, but intermediates also exist. In '*Lacerta*' *jacksoni* and *Adolfus alleni* some fibres of the ulnar nerve follow the 'lacertide' course while others follow the 'varanide' one, so that an independent ulnar nerve runs from the upper to the lower forelimb but receives additional fibres in the lower limb which form a slender bridge from the brachial trunk (Fig. 18b). '*Lacerta*' *echinata* and some *Adolfus africanus* are similar but more fibres follow the 'varanide' route, so that the bridge is thicker, and the upper part of the ulnar nerve more attenuated (18c). 82 *Lateral septum on bodenaponeurosis*. Present (0); absent (1).

Rieppel (1980) surveyed the jaw musculature of various scincomorph groups and believed that lack of a lateral septum on the bodenaponeurosis, and consequent lack of intersection of either the medialis or superficialis layers of the external adductor muscle, is a specialised feature of the Lacertidae. He is perfectly correct about this condition being present in the four species he examined, but a wider survey shows that it

is a minority state and most lacertids do have a lateral septum.

Behaviour

83 *Voice*. Usually mute (0); squeak frequently (1). See Böhme, Hutterer & Bings (1985).

84 *Copulatory position*. Male grasps female by flank (0); male grasps female by neck or mid-back (1).

Böhme and Bischoff (1976) regard holding the neck of the female during copulation as primitive in the Lacertidae, on the basis of the wide distribution of this behaviour in other lizards. However, the usual alternative, biting the flank, also has quite a broad distribution and in scincomorphs occurs in some Scincidae (for instance *Ablepharus*—Rotter, 1962) and Teiidae (*Cnemidophorus sexlineatus*—Smith, 1946; *C. gularis*—Walker, Cordes & Paulissen, 1987). So evidence from outgroup analysis is equivocal. Within the Lacertidae, neck biting is a rare and scattered condition suggesting it may be derived rather than primitive. It occurs in *Gallotia* (Böhme & Bischoff, 1976), *Psammodromus algirus* (Birkenmeier, 1951; Bosch, 1986), *Lacerta jayakari* (Böhme & Bischoff, 1976; Bischoff, 1981), *Lacerta vivipara* but only as a preliminary to grasping the flank (Mortensen, 1887), *Aporosaura anchietae* (Louw & Holm, 1972) and *Mesalina olivieri* (Bons, 1959). In *Psammodromus hispanicus* the flank may be grasped first and then the male holds the skin of the central back and sometimes further forward (In den Bosch, 1986). At least some other species of the holophyletic genus *Mesalina* grasp the flank of the female (*M. adramitana*, personal observations; *M. guttulata*, W. Ross, personal communication) and the use of outgroup analysis within the family, once the relationships of *Mesalina* and *Aporosaura* are established (p. 000), indicate that neck biting is derived in these groups. The same appears to be true in *Gallotia* and *Psammodromus algirus* (p. 000) and probably elsewhere.

METHODS OF ANALYSIS

As well as informal approaches, the data set (Appendix 2) was investigated by computer in two different ways: parsimony analysis and compatibility analysis.

Parsimony analysis

Parsimony analysis was carried out using the 2.4 version of the PAUP (Phylogenetic Analysis Using Parsimony) programme (Swofford, 1985). This produces one or more trees with the minimum number of character state changes (steps). It is a Wagner method of parsimony analysis in that forward and reverse changes have equal probability. The tree was rooted by the inclusion of a hypothetical common ancestor with 0 scores for all characters. When large numbers of taxa were analysed, the following options of the PAUP programme were initially used: ADSEQ = CLOSEST, HOLD = 25, SWAP = GLOBAL, MULPARS, ROOT = ANCESTOR, OPTIMISATION = MINF, BLRANGE, CSPOSS. ADDSEQ and HOLD options were subsequently varied, a process which sometimes produces shorter trees, but none were found. For less than 12 taxa the 'Branch and Bound' method of Hendy & Penny (1982) was employed, instead of GLOBAL

and MULPARS. For less than nine taxa the ALLTREES option was used, which is guaranteed to find minimum length trees. In some cases, where numerous alternative trees were found, consensus trees were computed using Swofford's CONTREE (Consensus Tree) programme. The option used was STRICT, which uses the 'strict' method of Rohlf (1982).

In parsimony analysis, variable scores have been treated in most cases as if they were primitive (0) scores, on the assumption that the existence of derived (1) scores in groups where both 0 and 1 occur is due to homoplasy. The only exceptions are cases where there is internal evidence within the taxonomic unit concerned that the primitive state in the group is 1. This is true of characters 3.1, 55, 64, 70 and 71 in *Meroles*, 70 and 71 in *Pedioplanis* (see Arnold, in press); and 15 in *Ophisops-Cabrita*.

In some cases, adjustment of variable scores makes characters invariant or results in only one taxon having the derived (1) condition. Such characters, where the derived state is not shared by two or more taxonomic units, contribute nothing to analysis and can be omitted. Thus, for the total Lacertidae, this is true for 20, 28, 36, 37, 40.1, 41.1, 41.2, 50, 51.2, 53.2, 54.2, 56, 57, and 76 ($n=14$), reducing the data set to 98 binary characters.

Compatibility analysis

Compatibility analysis was carried out using the programme of Gauld & Underwood (1986). This conducts Le Quesne tests (Le Quesne, 1969) on all characters in which both states occur more than once, and the frequency of failure of each character (that is incompatibility with other characters) is compared with that expected on a random basis. The characters are then ranked in ascending order of their randomness ratios, i.e. the ratio of observed incompatibilities to those expected on the null hypothesis of random distribution of the states of the characters. As already noted, it is not necessary to know the polarity of the characters concerned to do this.

Because the score of a reliable character may be adversely influenced by association with unreliable ones during the Le Quesne testing, a second procedure, known as 'boil down' is carried out. This removes the character with the highest randomness ratio and reruns the Le Quesne test and ranking procedure, often resulting in a different ranking order. Then, the character with the highest randomness ratio in this reduced set is removed and the process repeated, and so on until only a compatible set of the highest scoring characters is left. This set is expected to give good indications of relationship of the taxa concerned, provided it contains enough characters. Further information on relationships may be given by the inclusion of any additional characters that were not amenable to Le Quesne testing because the primitive state occurs in one taxon only. Other characters, considered in the reverse order of their removal during the 'boil down' procedure, may also contribute to analysis. In some cases, they can be substituted for members of the compatible set, or some small degree of homoplasy may be tolerated.

Some characters are likely to score badly during the initial 'boil down' because they are homoplastic. However, if a well substantiated subgroup of the one under investigation can be discerned, it is possible that a character present in the subgroup and outside it may give good information in one or both these areas in spite of its overall homoplasy. In such cases the relevant subgroups can be reanalysed separately.

Resolution of conflicts

Where parsimony and compatibility methods disagree, or when trees produced by parsimony differ from each other in detail, so there are alternative relationships for particular taxa, the evidence for the alternatives is compared. In attempting to resolve such conflicts, not only is the number of derived features on each side taken into account, but also their general lability, judged by the number of state changes the character makes in the total provisional lacertid phylogeny. Combining these factors involves a degree of subjectivity, but is more realistic than simply confining decisions to the number of binary characters supporting each version of relationships.

Comparison of methods of analysis

Parsimony and compatibility methods used here are in principle quite different. The Wagner parsimony approach aims to minimise the total number of steps in a tree and consequently minimises the number of homoplasies (parallelisms and reversals). The method is open to a number of criticisms as a means of estimating the phylogeny of a group. 1. To begin with, virtually all analyses of large systematic data sets involve considerable homoplasy, even when the method aims to minimise this. Given that homoplasy seems common in the evolution of animal groups, it is difficult to justify the lowest level as being most likely. 2. As all characters are given equal weight, it is possible that states correlating with the real course of evolution may sometimes be outweighed by labile homoplasious features, especially if these tend to be correlated. 3. The method sometimes produces a multiplicity of trees of equal length and there is no simple way of differentiating these. 4. Polarities have to be decided at the commencement of analysis. 5. With large numbers of taxa, the method cannot guarantee to find the shortest tree.

The compatibility method used here compares as follows. 1. There are no assumptions of how evolution proceeds, for instance, the method does not necessarily minimise homoplasy. 2. The method aims to differentiate compatible characters that are likely to show the structure of a phylogeny and to arrange the remainder in an order of increasing likely homoplasy, which means that the most noisy characters can be omitted from phylogeny reconstruction if required, so that swamping of real structure is less likely. 3. The method does not produce a multiplicity of trees. However, it often fails to provide a total structure for the phylogeny. 4. Only a few polarities need to be decided by external means (p. 215). 5. Like parsimony analysis, there is no guarantee that the shortest tree will be found. The compatibility method might be expected to fail in cases where most characters were somewhat homoplastic, so that only a small fully compatible set could be discerned, or none at all. Secondary analysis can sometimes alleviate this problem.

In the present case, parsimony and compatibility methods do not produce results that are radically different. As will be seen, in the Ethiopian and Saharo-Eurasian clade, where data show considerable order, both identify the same essential structure, although parsimony tends to show more detail. On the other hand, when dealing with primitive Palaeartic lacertids, in which there is considerable character conflict, both fail to make much impact, identifying the same relationships but failing to discern a robust general structure. So, in spite of their different rationales, the methods may not

necessarily differ much in result. This was also found in a detailed analysis of Equatorial African lacertids (Arnold, 1989).

PRELIMINARY DIVISION OF THE LACERTIDAE

Parsimony analysis of 98 characters for the whole Lacertidae produced over 100 trees of 333 steps and a consistency index of 0.294. The large number of trees indicates considerable homoplasy. Examination of a selection of these shows that *Lacerta jayakari* etc, all the Ethiopian taxa plus four advanced genera from Saharan and Eurasian areas, viz. *Acanthodactylus*, *Eremias*, *Mesalina* and *Ophisops-Cabrita*, from a clade which is derived from a paraphyletic assemblage of primitive Palaearctic and Oriental forms. This clade is relatively stable, but the arrangement of the remaining taxa is very variable. A consensus tree confirms this: the African and advanced section shows considerable structure, while little is discernible in the primitive Palaearctic and Oriental forms.

Fig. 19a

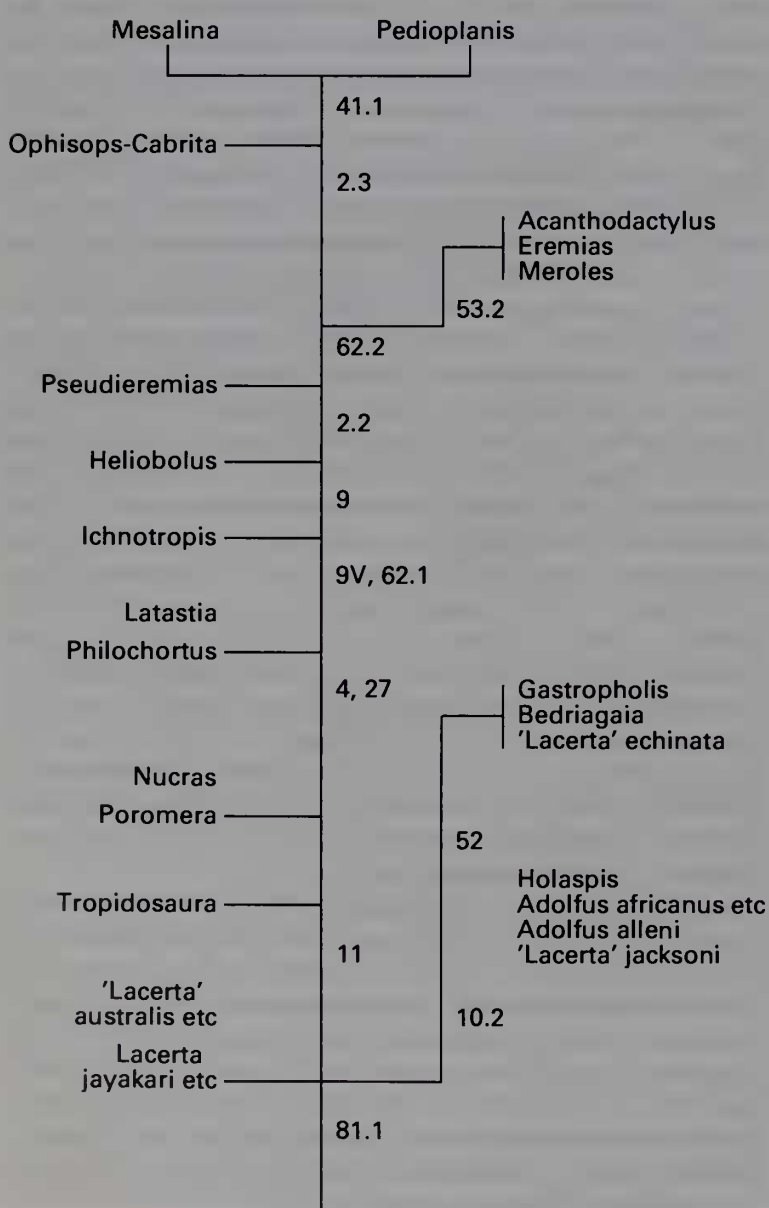
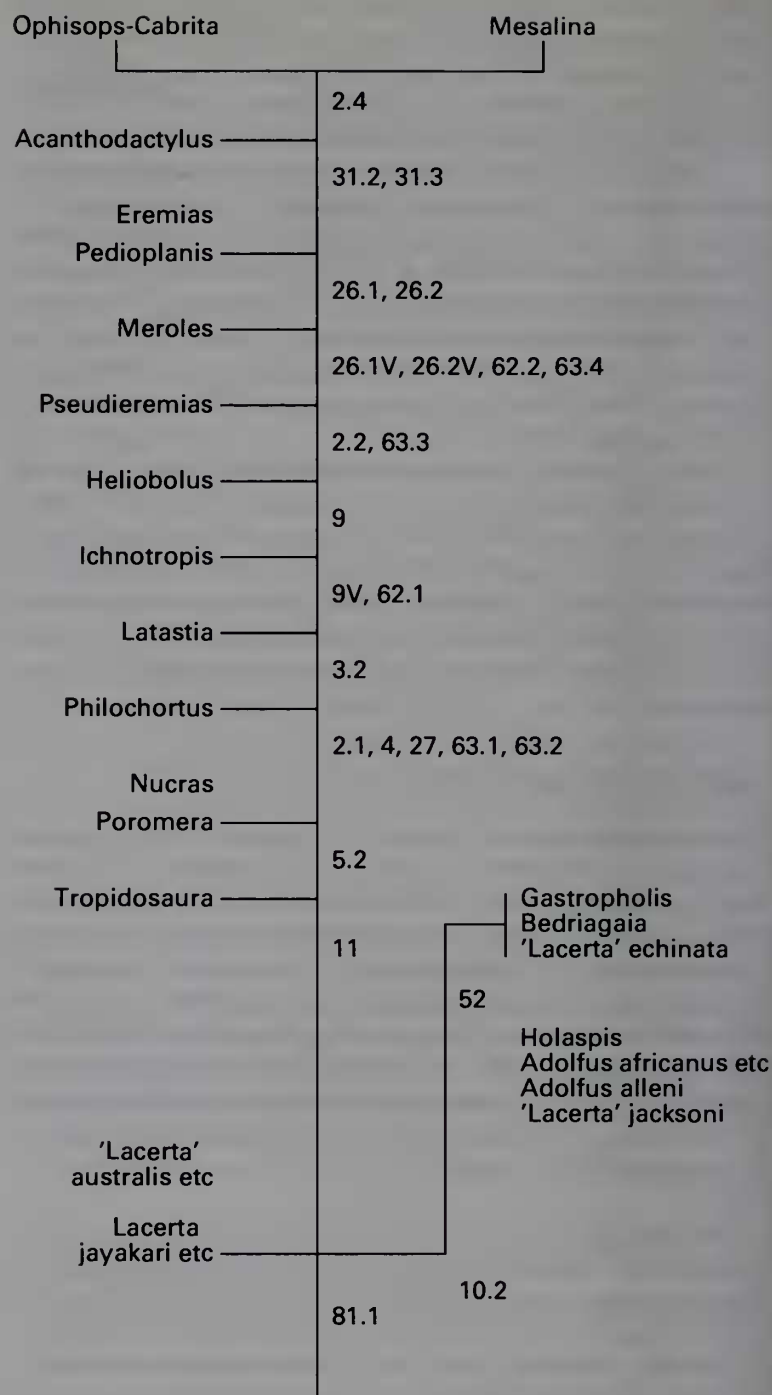


Fig. 19b



Compatibility analysis of the whole data set gives an overall randomness ratio of 0.87, again indicating that considerable homoplasy exists. The 'boil down' process produces a compatible set of 17 characters, with one alternative (53.1). This and three others (40.1, 43, 53.2) involve considerable numbers of variable (V) scores and are therefore discarded. The remaining characters generate the arrangement shown in Fig. 19a, which again associates *Lacerta jayakari* etc and all the Ethiopian and advanced Saharo-Eurasian taxa. In the remainder of the Lacertidae, the primitive Palaearctic and Oriental forms, compatibility produces no certain associations. This, like the variable results produced by parsimony analysis, indicates a lack of robust overall structure in the data set for these taxa.

The Lacertidae can therefore be divided into two sections for convenience: a holophyletic, mainly African group with advanced forms extending into Eurasia and a primitive Palaearctic and Oriental assemblage that is very probably paraphyletic. These will be analysed further separately.

Fig. 19c

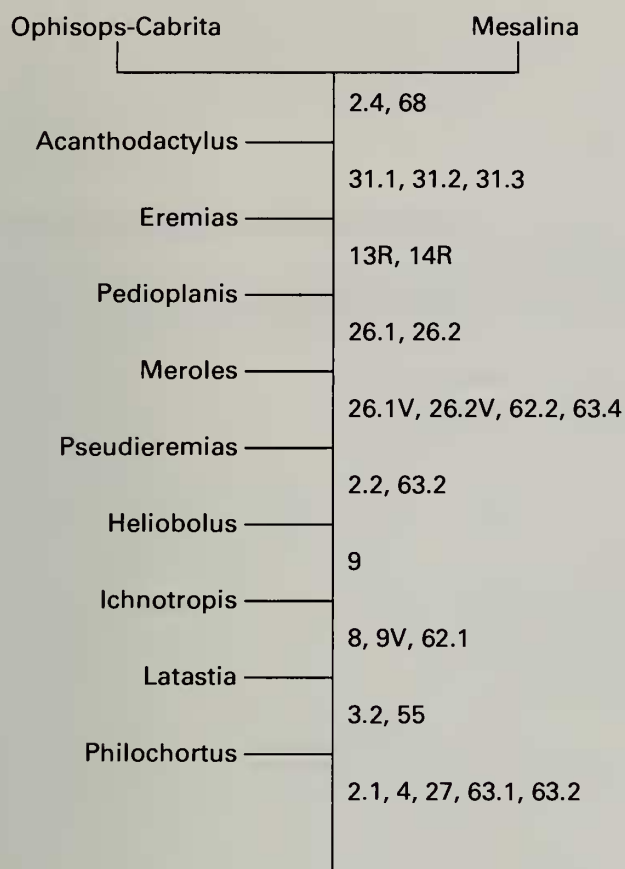


Fig. 19 Compatibility analyses of the Lacertidae. a. Total lacertids; b. Ethiopian and advanced Saharo-Eurasian forms; c. *Philochortus* and its derived relatives. V – variable characters

PRIMITIVE PALAEARCTIC AND ORIENTAL LACERTIDS

Parsimony analysis

Parsimony analysis was applied to the primitive Palearctic and Oriental lacertids with a hypothetical ancestor of the Ethiopian and advanced Saharo-Eurasian clade included in the data set. Characters that have no shared derived states within this assemblage were eliminated, namely 2.2, 2.3, 2.4, 3.2, 4, 5, 6.1, 6.2, 7, 8, 9, 10.1, 10.2, 11, 13, 14, 15, 16, 17, 20, 21, 23, 25, 26.2, 26.3, 27, 28, 34, 36, 37, 40.1, 40.2, 41.1, 41.2, 45.3, 49.1, 49.2, 50, 51.1, 51.2, 52, 53.1, 53.2, 54.1, 54.2, 55, 56, 57, 62.1, 62.2, 65, 69.2, 74, 75, 76, 81.2. This left a set of 56 binary characters. Over 100 trees of 134 steps and a consistency index of 0.410 were produced.

As the evidence for polarities of some characters involves a marked degree of conflict, particularly between outgroup and other indicators (p. 215), the process was repeated with the following polarities changed. Run 2: characters 22.2, 28, 32 and 43. Run 3: characters 22.2, 28, 31.2, 31.3, 32, 43 and 84. Run 4: characters 22.1, 22.2, 28, 31.1, 32 and 43. All these modifications produced trees with more steps than those in which the original polarities were used, so the latter may well be correct. Characters 22.2, 32 and 43 turn out to be substantially homoplasious, which suggests they are quite labile in lacertids and that the outgroup indicators of polarity could be wrong (p. 214).

As expected from the preliminary analysis of the whole

Lacertidae, a consensus tree derived from the latter has relatively little structure with a basal polychotomy of 14 branches. The only associations are *Gallotia*, *Psammmodromus*, *Lacerta parva* etc. and *L. brandtii*; *Lacerta princeps* with *L. lepida* etc. and these with the *Lacerta agilis* group; *Lacerta dugesii* with *L. perspicillata*; *Lacerta graeca* with *L. oxycephala*; and *Lacerta jayakari* etc. with the hypothetical ancestor of the Ethiopian and advanced Saharo-Eurasian clade.

Examination of a selection of the numerous trees produced by parsimony analysis, both with original and modified polarities, shows that, while not necessarily universal and therefore not represented in consensus trees, certain additional associations are very frequent; for instance, *Podarcis*, *L. andreanskyi*, the *L. dugesii*-*L. perspicillata* clade, *L. danfordi* and *L. laevis*.

Compatibility analysis

Again, this method fails to produce a robust detailed picture of relationships but, like parsimony, supports the *Gallotia*-*Psammmodromus* association strongly and allies these with *L. parva* etc. and *L. brandtii*. It also allies *L. dugesii* with *L. perspicillata*, *L. graeca* with *L. oxycephala* and *L. jayakari* with the Ethiopian and advanced Saharo-Eurasian clade. In addition, *L. vivipara* is associated with the latter groups.

Karyological and biochemical evidence

The lack of consistent structure in the data set for primitive Palearctic lacertids probably results from the amount of morphological change which has occurred being relatively restricted and often repetitive, so that there are high levels of homoplasy. Given the poor quality of the evidence from general morphology, other sources of information must also be considered. Although gross karyology is often uninformative in lacertids (see for example Kupryanova, 1986), it is not always so and interesting information on the fine structure of lacertid chromosomes has also recently been reported, particularly C-banding, chromosome number and the location of the nucleolar organiser (Odierna, Olmo & Cabror, 1985; Olmo, Odierna & Cabror, 1986; Odierna, Olmo & Cabror, 1987; Cano, Baez, Lopez-Jurado & Ortega, 1984; Lopez-Jurado, Cano & Baez, 1986). Some well supported species groups seem to be consistent for the latter feature, but it is not possible to be sure when the condition can be regarded as a synapomorphy, as the primitive state is not certainly established. This is also true for chromosome numbers, where it has been suggested that the high counts of 40 and 42 found in some *Takydromus sexlineatus* and 40 in *Gallotia* are primitive relative to the 38 chromosomes present in most lacertids that have been checked, although distribution of other features suggests the reverse. A wider survey of these characters in the Lacertidae may resolve matters.

Attempts have also recently been made to determine relationships of lacertids, especially primitive Palearctic ones, by chemical means including protein electrophoresis and immunology, particularly of albumins (Engelmann & Schäffner, 1981; Engelmann, 1982; Guillaume and Lanza, 1982; Lanza and Cei, 1977; Lanza, Cei and Crespo, 1977; Lutz and Mayer, 1984, 1985; Lutz, Bischoff and Mayer, 1986; Mayer, 1981, 1986. Mayer and Tiedemann, 1980a, 1980b, 1981, 1982; Borisov & Orlova, 1986; Busack & Maxson, 1987). In some cases, this chemical evidence supports

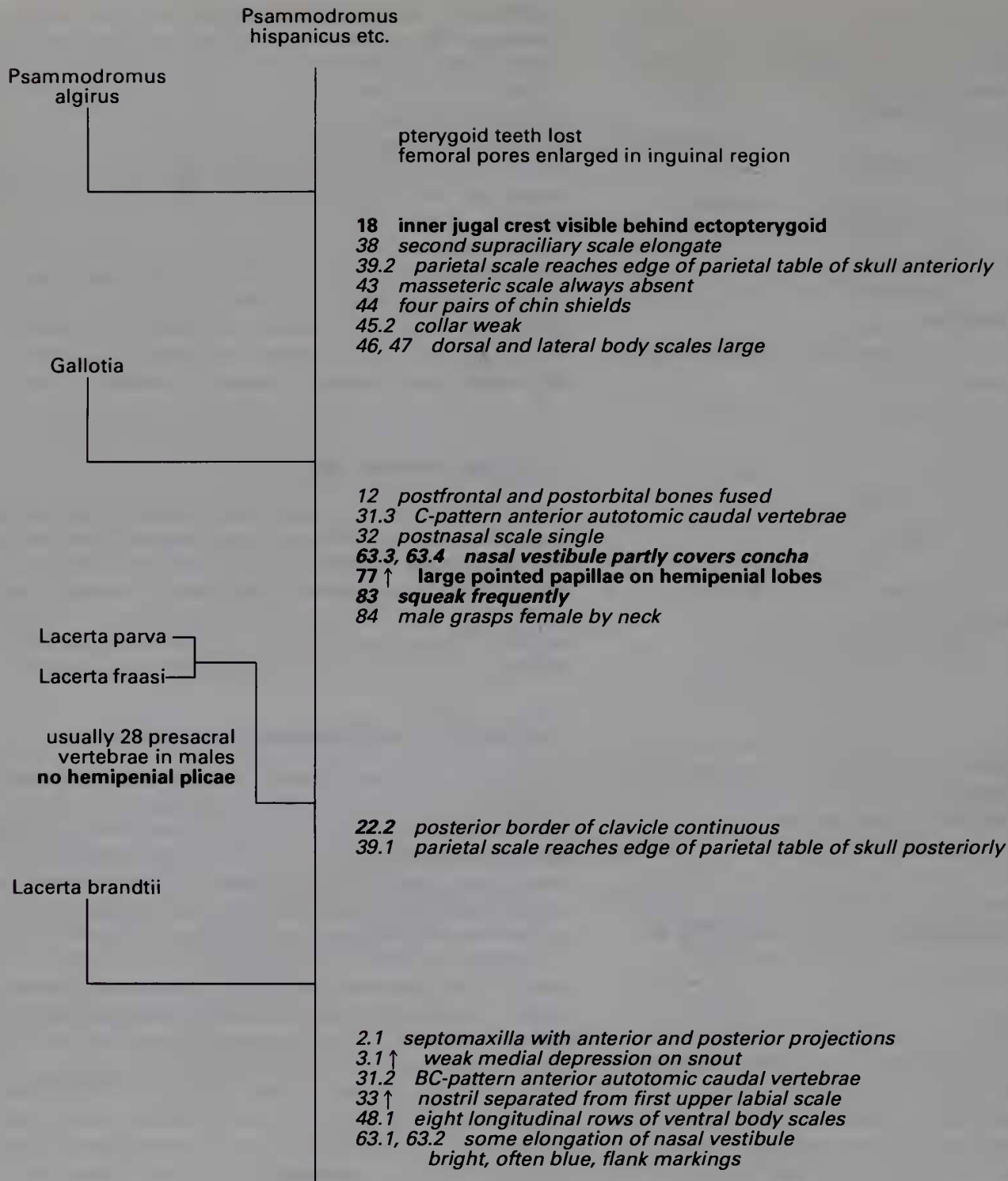


Fig. 20 Relationships of *Psammodromus*, *Gallotia*, *Lacerta parva* etc and *Lacerta brandtii*. Character transformations supporting relationships are differentiated as follows.

bold—transformation unique in lacertids

bold italic—transformation unique in primitive Palaearctic and Oriental lacertids

roman—transformation occurring more than once in primitive Palaearctic lacertids, but not in Ethiopian and advanced Saharo-Eurasian forms.

roman italic—transformation occurring more than once in primitive Palaearctic lacertids and also in Ethiopian and advanced Saharo-Eurasian forms.

↑ — character that subsequently reverses

R — character reversal

groupings established on the basis of morphology but it sometimes conflicts with them. Also, alternative interpretations of the results have been suggested (Busack & Maxson, 1987). The following discussion, while based largely on morphology, take these new karyological and chemical data into account.

Gallotia, *Psammodromus* and their likely relatives

Both compatibility analysis and parsimony techniques associate these forms in the way shown in Fig. 20, in which a few characters additional to the basic lacertid data set have been incorporated. The relationship of *Gallotia* and the species of *Psammodromus* is quite strongly supported and there is also limited corroborative evidence from protein electrophoresis (Lutz, Bischoff and Mayer, 1986). *P. algirus* lacks the distinctive large pointed papillae on the hemipenial lobes (77) of other *Psammodromus* and *Gallotia*, but this may well be a secondary loss, perhaps associated with the narrowing of the hemipenial lobes found in this species (Arnold, 1973, 1986a).

A direct relationship between the *Psammodromus hispanicus* group and the markedly different *P. algirus* is also supported by several features, in particular the unique modified jugal (18), and also the elongate second supraciliary scale (38) and the presence of only four pairs of chin shields (44); while not unique, these latter characters have a very restricted distribution among primitive Palaearctic lacertids. The available immunological evidence for this association is weak and protein electrophoresis does not suggest that the two sections of *Psammodromus* are closer to each other than each is to *Gallotia* (Lutz, Bischoff and Mayer, 1986).

In fact there are a number of characters that support a direct relationship between *P. algirus* and *Gallotia*, including lack or poor development of a septum on the bodenaponeurosis (82), long hemipenial lobes (72), hemipenial micro-ornamentation of simple spines (78.2), ten or more longitudinal rows of ventral scales (48.2), and perhaps a reversion to a primitive feature, contact between the nostril and the first upper labial scale (33). However, fewer characters support this association than that between the two parts of *Psammodromus* and all of them occur elsewhere among primitive Palaearctic lacertids. Ten longitudinal rows of ventrals could easily be derived from the eight found in other *Psammodromus*. While not being interpreted as supporting a direct relationship between *P. algirus* and *Gallotia*, these presumed parallelisms emphasize the general affinity of the latter and the whole of *Psammodromus*.

It has been suggested that many of the features of *Gallotia*, and consequently of *Psammodromus*, are plesiomorphic (Böhme, Hutterer & Bings, 1985). As such they could not be used to support relationships. However, when polarities were altered for these characters (Run 3, p. 231) and parsimony analysis carried out, *Gallotia* and *Psammodromus* were still firmly associated and neither was placed near the base of trees produced.

The holophyly of *Gallotia* is quite well supported, but relationships within the genus involve a conflict between morphology and chemical evidence. *G. galloti*, *G. simonyi* and *G. stehlini* have most apparent physical synapomorphies (Fig. 21), while *G. atlantica* shares only ossification of the temporal scales (19) with the two latter species, and only lateral extension of the parietal scale (39.2) with *G. galloti*. In contrast, albumin immunology and protein electrophoresis suggest that the closest relationship is between *G. atlantica*

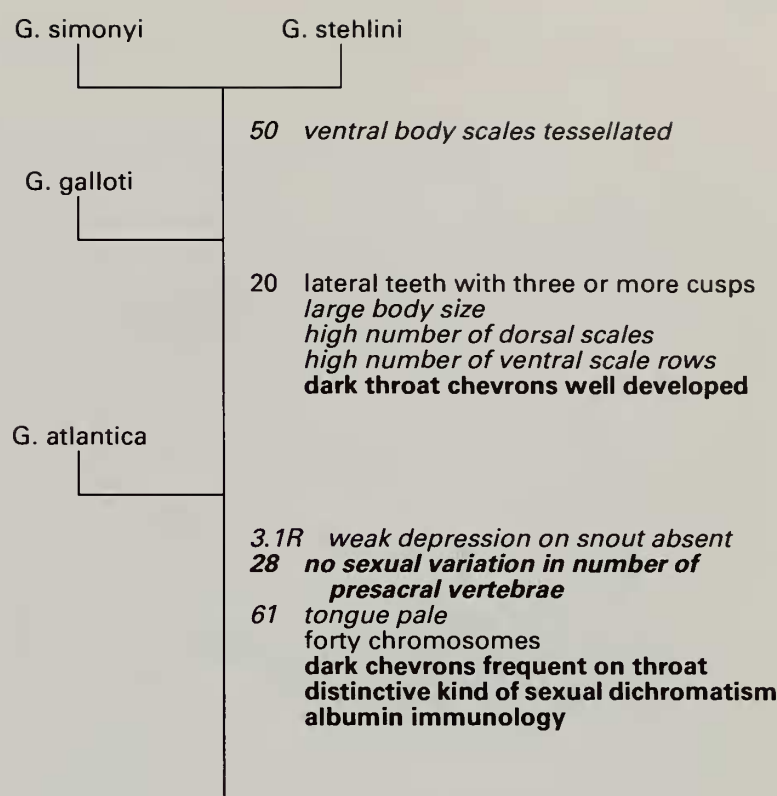


Fig. 21 Relationships of the species of *Gallotia*. For further explanation, see caption of Fig. 20

and *G. galloti* (Lutz, Bischoff & Mayer, 1986). A preliminary numerical phylogenetic analysis was conducted by Thorpe, Watt and Baez (1985), who constructed a Wagner tree based on the range coded means of 23 scalation and 24 adjusted body proportions for *G. atlantica*, *G. galloti* and *G. stehlini*. A mid-point rooted cladogram indicates that *G. galloti* and *G. stehlini* are most closely related, but the authors regard the result as equivocal.

Engelmann and Schäffner (1981), on the basis of immunoelectrophoresis, suggest that *L. parva* is related to *L. princeps* and *L. lepida*, but morphology supports relationship with *Psammodromus* and *Gallotia*. Features 22.2 and 39.1 (and possibly 78.1) associate *L. parva* etc. with *Gallotia* and *Psammodromus*, while absence of inscriptional ribs (30) and nostril separated from first upper labial (if not treated as a character that reverses elsewhere in the assemblage) suggest that *L. parva* and *L. brandtii* are sister species. However these latter features are more homoplasious and the first relationship is preferred.

Lacerta lepida etc., *L. princeps* and the *L. agilis* group

Biochemical evidence (Engelmann and Schäffner, 1981; Lutz and Mayer, 1984) indicates a close relationship between *L. princeps* and *L. lepida*. This presumably also applies to *L. pater*, which has only recently been demonstrated to be specifically distinct from *L. lepida* (Bischoff, 1982). Relationship is also supported by the presence of a derived karyotype in both *L. lepida* and *L. princeps* of $2n = 36$, instead of the usual lacertid $2n = 38$ (Rykena and Nettman, 1986). The three species also share some derived, although not unique, morphological features including fused postorbital and post-frontal bones in adults (12), frequently very large occipital scale (40.1), prominent blue spots on the flanks and a hemipenial micro-ornamentation of simple hooked spines (78.2).

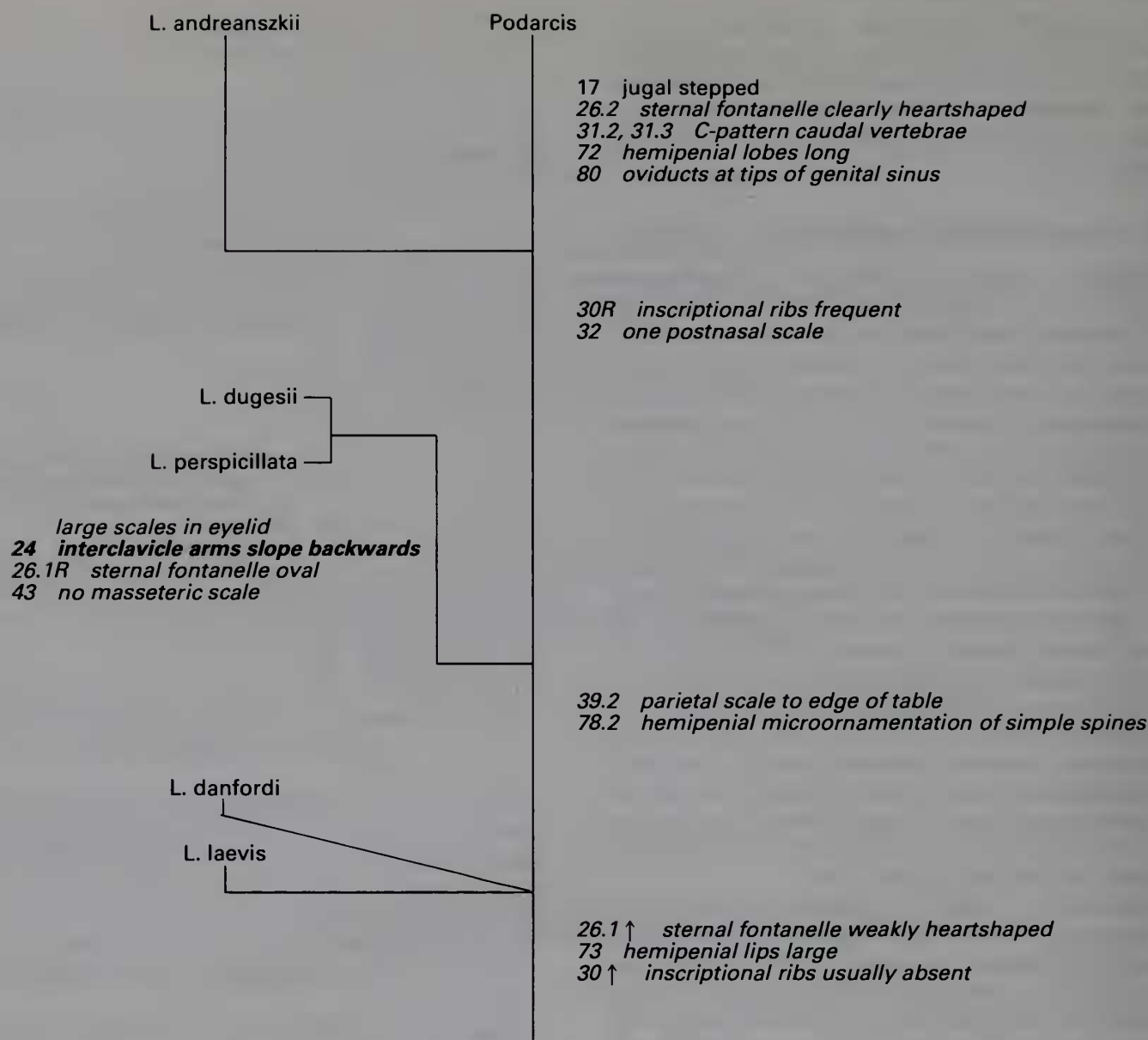


Fig. 22 Relationships of *Podarcis* and its possible relatives.

Characters 31.2, 31.3 and 72 found in *Podarcis* are paralleled in *Lacerta danfordi* etc. For further explanation, see caption of Fig. 20

L. lepida, *L. pater* and *L. princeps* have often been associated with the *Lacerta agilis* group, for instance by Boulenger (1920) and Arnold (1973), but other authors have placed some or all of them close to *Gallotia* (Peters, 1961; Böhme, 1971). In fact, morphological and biochemical evidence does not corroborate this latter view, and albumin immunology and protein electrophoresis (Lutz and Mayer, 1984) suggest that *L. lepida* and its relations are more closely allied to *Podarcis*, the archaeolacertas and *L. graeca* than they are to the *Lacerta agilis* group. However, there is no obvious supporting morphological evidence here either. Instead, a non-unique series of derived features is shared with the *Lacerta agilis* group, including large adult size, usual ossification of the temporal scales (19), no septum on the bodenaponeurosis (82), frequent green dorsal colouring, no bright belly colour and no blue spots on the outer ventral scales (60). *L. lepida* and its two close relatives also share a distinctive growth pattern with the *Lacerta agilis* group in which hatchlings are very 'embryonic' with a very large rounded head and short extremities, and head length shows strong allometric increase in adult males. These growth characteristics do not occur in other large lacertids, such as *Lacerta jayakari* or the species of *Gallotia*. *L. lepida*, *L.*

princeps and members of the *L. agilis* group that have been checked all share a similar chromosomal position for the nucleolar organiser (Odierna, Olmo & Cabror, 1987) but, as noted (p. 231), it is not yet clear whether this is a derived feature.

Within the *Lacerta agilis* group, immunology and overall morphological resemblance associate the members of the *L. viridis* assemblage closely (that is all members of the *L. agilis* group except *L. agilis* itself). *L. agilis* lacks the temporal ossification (19) of these forms and has a distinctive high presacral vertebral count (Arnold, 1973) but appears to be their sister taxon. This relationship is supported by a frequent step in the lower border of the outer face of the jugal bone (17) and a tendency for narrow light stripes in the dorsal pattern of some individuals. Another indication of the close affinity of these species is that hybrids between many of them can be produced in captivity (see summaries in Böhme, 1984 and Rudyk, 1986).

L. schreiberi of Spain and Portugal is usually regarded as close to *L. viridis* and electrophoresis appears to support this (J. Mateo, personal communication). It differs in less frequently having a stepped jugal border and in always lacking narrow light stripes, both probably primitive features in which it resembles the *L. lepida*-*L. pater*-*L. princeps* assemblage.

lage. Like some members of this, *L. schreiberi* has the postorbital and postfrontal bones regularly fused (12) and is also similar to them in the often fairly large occipital (40.1), the presence of more than six longitudinal rows of ventral scales (48.1), a frequently small preanal scale, and a prominent pattern of light spots, at least laterally, in juveniles. However, all except the first of these features also occur within the *L. viridis* assemblage, in the *L. trilineata* complex (*L. trilineata*, *L. media* and *L. pamphylica*). Furthermore, *L. schreiberi* lacks the distinctive karyotype of *L. lepida* and its relatives, having instead the primitive number ($2n = 38$) found in *L. viridis* (J. Mateo, personal communication). The position of this species is therefore somewhat equivocal.

***Podarcis* and its likely relatives**

Arnold (1973) pointed out various similarities between *Podarcis* and *Lacerta andreanszkii*, *L. dugesii*, *L. perspicillata*, *L. danfordi* etc and *L. laevis*. It was suggested that *Podarcis* might be most closely related to the first three of these, in particular *L. andreanszkii*. Richter (1980) formalised some relationships using these data, associating *L. perspicillata* and *L. dugesii*, making them the sister group of *Podarcis* s. str. and transferring them to *Podarcis* s. lat. The parsimony consensus tree for primitive Palaearctic and Oriental lacertids associates only *L. perspicillata* and *L. dugesii*, as does compatibility analysis but, as noted, examination of a sample of the more than a hundred alternative trees produced for this assemblage by parsimony analysis shows that the species are frequently associated in the way shown in Fig. 22. Parsimony analysis of just *Podarcis* and these likely relatives produces the same arrangement.

The association of *L. laevis* and *L. danfordi* etc with the rest of the species in Fig. 22 is weak, being based only on the hemipenial lips being large (73), the weakly cordate sternal fontanelle (26.1) and the lack of inscriptional ribs (30). All these reverse subsequently and the last character is widespread elsewhere in the primitive Palaearctic lacertids. *L. danfordi* etc parallels *Podarcis* in two further features, paired transverse processes on the anterior automatic vertebrae (31.2) and long hemipenial lobes (72), which may be some indication of affinity.

Overall relationships among the species of *Podarcis* are difficult to discern from morphology, as the taxa are all very similar in this respect. However, the presence of broad outer sulcal lips on the hemipenial lobes in *Podarcis erhardii* and *P. peloponnesiaca* suggests they are closely related (Arnold, 1973), something which has recently been confirmed by electrophoresis (Mayer, 1986). This technique also demonstrates the affinity of *P. milensis* and *P. gaigiae* (Mayer & Tiedemann, 1980b) and immunology indicates the near relationship of *P. filfolensis* and *P. wagleriana* (Lanza & Cei, 1977). The members of each of these species pairs have geographical ranges that are close to one another. A broad immunological study (Lutz & Mayer, 1985) suggests that all these forms plus *P. tiliguerta* and *P. taurica* may be fairly closely related. *P. melisellensis* seems to stand apart on this evidence, although protein electrophoresis and morphology indicate it might be close to *P. taurica*. Immunology, places *P. sicula* and *P. muralis* outside a group constituted by all the foregoing forms. Certainly, a primitive position for *P. muralis* would not be unlikely, as this species, and *P. bocagei* and *P. hispanica*, lack a derived feature of the hemipenis found in all other *Podarcis*, namely attachment of the outer sulcal lips to

the walls of the hemipenial lobes so they cannot be reflected (Arnold, 1973).

Archaeolacertas etc. and *Algyroides*

The term archaeolacerta was first used by Méhely (1909) for palaearctic *Lacerta* species in which the skull is depressed and lightly ossified with fenestrated supraocular osteoderms and often no pterygoid teeth; dorsal scales are often flat and smooth and the tail slender and fragile. These features, which vary greatly in their development, appear to be functionally related to the problems of survival in rocky habitats and of using crevices as refuges (Arnold, 1973). Given their apparent lability, these derived morphological characteristics of archaeolacertas, an assemblage which is otherwise generally primitive, do not provide very strong evidence for monophyly, especially as they occur independently in such forms as *Lacerta cyanura*. However, there is biochemical evidence for the affinity of some of the species. Protein electrophoresis associates *L. horvathi*, *L. oxycephala* and *L. graeca* (Mayer and Tiedemann, 1982) while albumin immunology indicates that the first two are related to *L. bedriagae* but separates *L. graeca*, which is as distinct from the others immunologically as they are from *Podarcis* (Lutz and Mayer, 1985). Immunology also indicates that *Lacerta saxicola*, *L. dejugini* and perhaps *L. paraticola* are more closely related to each other than they are to *Lacerta vivipara*, the *Lacerta agilis* group and *Podarcis* (Borisov & Orlova, 1986).

The great interspecific variability of the morphological features of archaeolacertas makes it difficult to define the borders of the group by this means and evidence for membership may conflict. As we have seen *L. graeca* is separated by albumin immunology but the results of protein electrophoresis are nearly identical for this species and *L. oxycephala*. The two also share a derived feature not found elsewhere in the primitive Palaearctic lacertids, namely expanded scales bordering the ventral mid-line of the tail (58), and are also able to hybridise in captivity (Mertens, 1950). Again *L. danfordi* etc has some archaeolacerta features but also similarities to *Podarcis* and its apparent relations.

The species regarded as archaeolacertas can be divided into three main groups which may form a sequence. 1. *L. graeca* and *L. oxycephala*, which have the apparently primitive arrangement of two superposed postnasals but expanded subcaudals. 2. More northern and western forms, like *L. mosorensis*, *L. horvathi*, *L. monticola* and *L. bedriagae* in which the postnasal condition appears to be more derived and often variable, some or all individuals having a single postnasal with or without the supranasal contacting the loreal above it, and the rostral often contacting the frontonasal. 3. The *L. saxicola* complex centred in the Caucasus area, the members of which nearly always have a single large postnasal, usually no supranasal-loreal contact and high presacral vertebral counts (commonest numbers: 27 in males, 28 in females). There is evidence that species of this last group have hybridised extensively (Darevskii, 1967), another indicator of close relationship. If the physical features said to characterise archaeolacertas are set aside, they show close resemblance to some other *Lacerta* species found in and around the Caucasus, such as *L. chlorogaster*, *L. derjugini* and *L. praticola*. Most of the resemblance is in primitive characters but these forms share the single postnasal and high presacral vertebral numbers of members of the *L. saxicola* complex and are probably closely related to them. As noted, immunology

gives further support in the case of *L. derjugini* and perhaps *L. praticola*.

In general, archaeolacertas are similar to *Podarcis* and its apparent relatives (p. 235) and *Algyroides*. Most of this resemblance is plesiomorphic. They share posterior extension of the parietal scale to the edge of the parietal table of the skull (39.1), but this is also present in the *L. parva-Psammodromus-Gallotia* assemblage. However, immunology suggests *Podarcis* and some archaeolacertas are quite closely related (Lutz and Mayer, 1984; Lutz, Bischoff and Mayer, 1986). There is nevertheless, no evidence for the idea that archaeolacertas were derived polyphyletically from within *Podarcis*, as suggested by Boulenger (1920) and Klemmer (1957).

L. jayakari etc, *L. cappadocica*, *L. vivipara* and *Takydromus*

Parsimony and compatibility treatments confirm the association of *L. jayakari* etc. with the Ethiopian and advanced Saharo-Eurasian clade. No other taxon is consistently and directly associated with these forms but, in many of the alternative parsimony trees produced when the primitive Palaeartic and Oriental lacertids were analysed, *Takydromus* etc., *Lacerta cappadocica* and *L. vivipara* were often connected to them. Parsimony analysis restricted to all the foregoing taxa produces five alternative trees with a consistency of 0.795, all again making *Lacerta jayakari* and the Ethiopian and advanced clade sister groups, but associating these and the other taxa in a variety of ways.

As noted by Boulenger (1921) the primitive members of the distinctive East Asian genus *Takydromus* have considerable similarity to *Lacerta vivipara*. *Takydromus* etc. shares more states with this species than with any other taxon, although these vary in their development and consistency and none is unique (Table 1). This resemblance is not emphasised in parsimony analysis because some of the characters concerned are variable within one or both taxa, being consequently scored as 0 rather than 1 (see p. 229), and so do not contribute to assessments of relationship. In some parsimony treatments, *L. vivipara* is often associated with *L. andreanskyi*, the two sharing characters 32, 35, 39.1, 39.2 and 60. But, resemblance to *Takydromus* etc. in derived features is greater and may indicate a real relationship.

If the polarity of some characters, where the evidence for the primitive state conflicts, is changed (run 4, p. 231), *Takydromus* etc. is associated with *L. cappadocica* and sometimes *L. vivipara* in a proportion of the alternative trees produced by parsimony methods. However, as already noted, the trees concerned have more steps than those where polarities are unaltered.

General relationships

As already seen, the affinities of taxa within the groups discussed above are often equivocal and this is even more marked when overall relationships among primitive Palaeartic lacertids are considered. Neither parsimony nor compatibility treatments of morphological data give a detailed and consistent pattern of relationships but, when original polarities are used, trees produced by parsimony often have two main branches. One of these includes *Takydromus* etc., *L. cappa-*

Table 1 Apparent synapomorphies of *Takydromus* and *Lacerta vivipara*

	<i>Takydromus</i>	<i>Lacerta vivipara</i>
Anterior descending processes of frontal bone reduced (6.1)	+	often
Postorbital and postfrontal bones fused (12)	+	+
Loop of clavicle continuous (22.2)	+	most cases
A pattern caudal vertebrae (31.1)	+	+
Single postnasal scale (32)	usual	+
Supranasal and loreal scales often in contact (35)	+	+
Parietal scale to edge of parietal table (39.2)	often	+
Femoral pore row reduced (51.1)	+	sometimes
Retractor lateralis anterior broad in front of vent, often joining its anterior lip (67)	+	+
Hemipenial sheath very weak	+	+

docica, *L. jayakari* etc. and the African and advanced Saharo-Eurasian clade, *L. lepida* and *L. princeps*, the *L. agilis* group and often *L. vivipara* as well; the other branch includes everything else. The arrangement is also frequent with some polarity modifications (runs 2 and 3, p. 231). However, evidence for the reality of the two branches is weak, the first being supported consistently only by character 60 and the second by 39.1. Also, relationships within the two assemblages show great variation. This general pattern is shown in Fig. 23.

In an attempt to clarify relationships among the western Palaeartic lacertid groups, comparative albumin immunology has been carried out on *L. cappadocica*, *L. jayakari*, *L. vivipara*, *L. bedriagae*, *L. graeca*, *Podarcis*, members of the *L. agilis* group, *Psammodromus* and *Gallotia* (Lutz & Mayer, 1985; Lutz, Mayer & Bischoff, 1986). These studies associate *L. cappadocica* with *L. graeca*, *L. bedriagae* and *Podarcis*, while *L. jayakari* may be connected here or just possibly with the *L. agilis* group. In one study, there is no indication of a very close connection of any of these forms with *Lacerta vivipara* (Lutz, Bischoff & Mayer, 1986) but it is associated with the *L. agilis* group in the other (Lutz & Mayer, 1985). All these forms are immunologically closer to each other than they are to *Psammodromus* and *Gallotia*.

It is apparent from the foregoing discussion that the higher relationships of primitive Palaeartic lacertids are by no means clear. Morphological data does not give an unequivocal pattern and differs considerably from that derived from immunology. The latter is incomplete in its coverage and some of the data is open to different interpretations (Busack & Maxson, 1987). Biochemical and karyological data must be more comprehensive and additional sources of evidence, such as DNA sequencing, need to be investigated if relationships are to be elucidated. However, if the main branching events in the phylogeny occurred swiftly, without much evolutionary change between dichotomies, comprehensive reconstruction of the cladogenetic history of primitive Palaeartic and Oriental lacertids may not be possible.

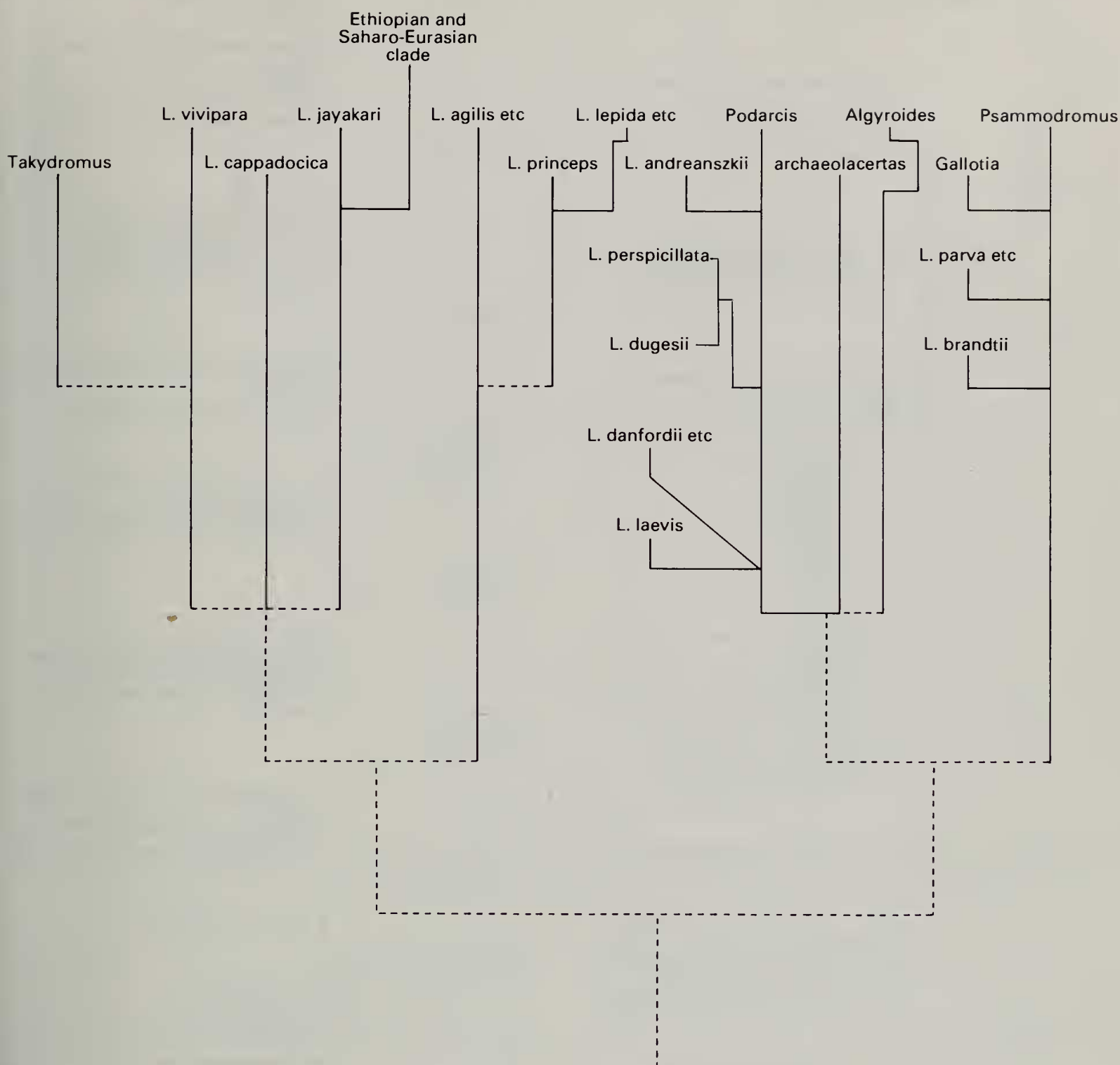


Fig. 23 Putative relationships of primitive Palaeartic lacertids based mainly on morphology. Interrupted lines indicate the more tentative associations. Albumin immunology separates *Gallotia* and *Psammmodromus* from the rest.

ETHIOPIAN AND ADVANCED SAHARO-EURASIAN FORMS

Parsimony analysis

Characters which have no shared derived states within the group made up of *Lacerta jayakari* etc. and the Ethiopian and advanced Saharo-Eurasian forms were eliminated. In addition to those listed on p. 229, these were 17, 18, 22.1, 24, 25, 35, 38, 43, 51.1, 58, 67, 70, 72, 73, 77, 78.1, 81.1, 82, 83, and 84, reducing the data set to 78 characters. Parsimony analysis was then carried out, resulting in four alternative trees of 196

steps and a consistency index of 0.398. These trees are not much different from the relevant section of the consensus tree for the whole Lacertidae and very similar to the estimate of phylogeny finally preferred (Fig. 24). Most taxa are arranged along a single stem with a separate branch near the base containing *Adolfus africanus* etc., *A. alleni*, *Bedriagaia*, *Gastropholis*, *Holaspis*, '*Lacerta*' *echinata* and *L. jacksoni*, which will be referred to as the Equatorial African clade. On the main stem, *Philochoortus* and its more derived relatives, lying above it on the tree, form a distinct group specified by a relatively large number of synapomorphies. Most of the tree topology is constant, but *Pedioplanis* and *Eremias* appear either as successive branches or as sister groups, and within

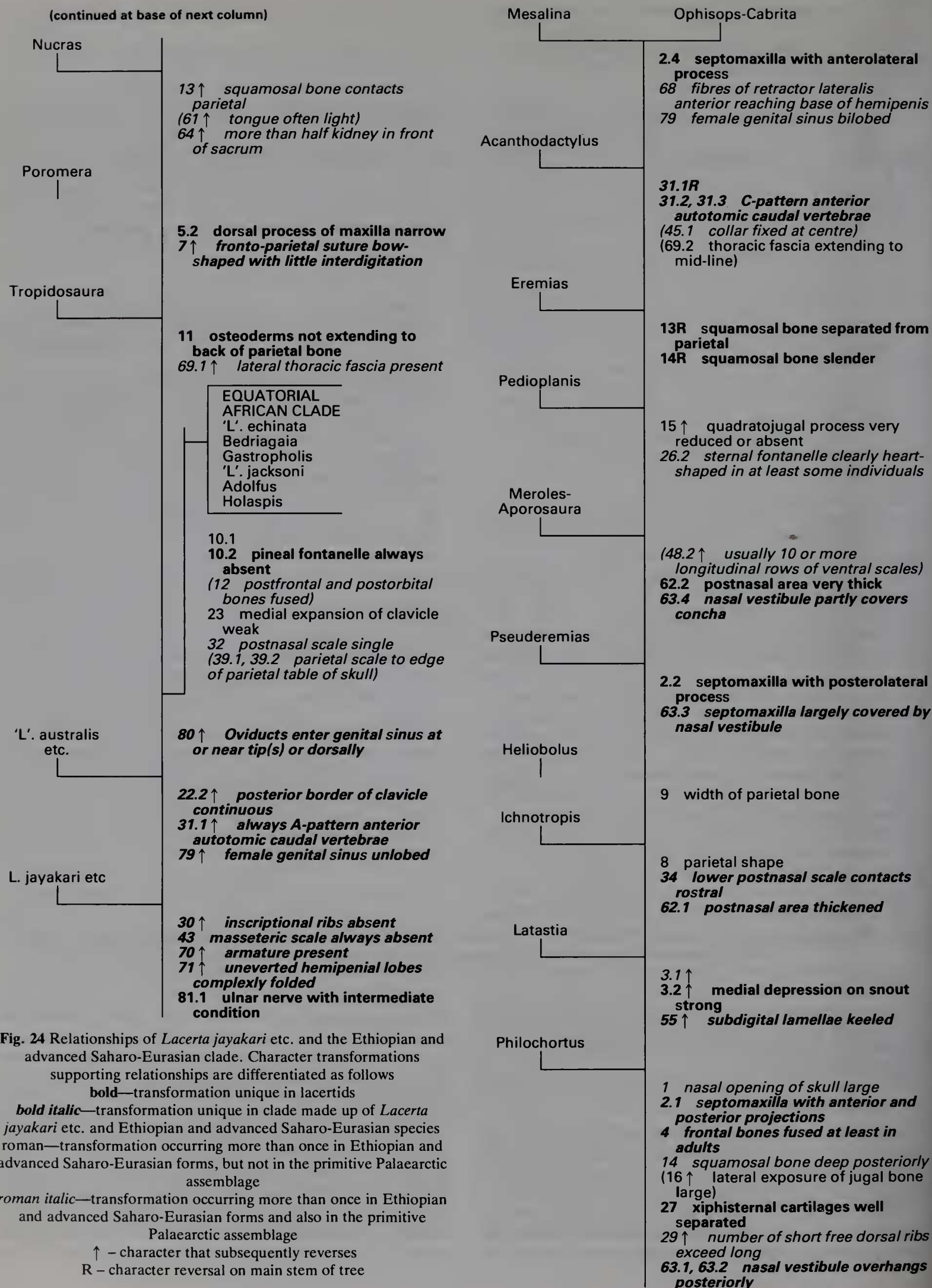


Fig. 24 Relationships of *Lacerta jayakari* etc. and the Ethiopian and advanced Saharo-Eurasian clade. Character transformations supporting relationships are differentiated as follows

bold—transformation unique in lacertids

bold italic—transformation unique in clade made up of *Lacerta jayakari* etc. and Ethiopian and advanced Saharo-Eurasian species
 roman—transformation occurring more than once in Ethiopian and advanced Saharo-Eurasian forms, but not in the primitive Palearctic assemblage

roman italic—transformation occurring more than once in Ethiopian and advanced Saharo-Eurasian forms and also in the primitive Palearctic assemblage

↑ — character that subsequently reverses

R — character reversal on main stem of tree

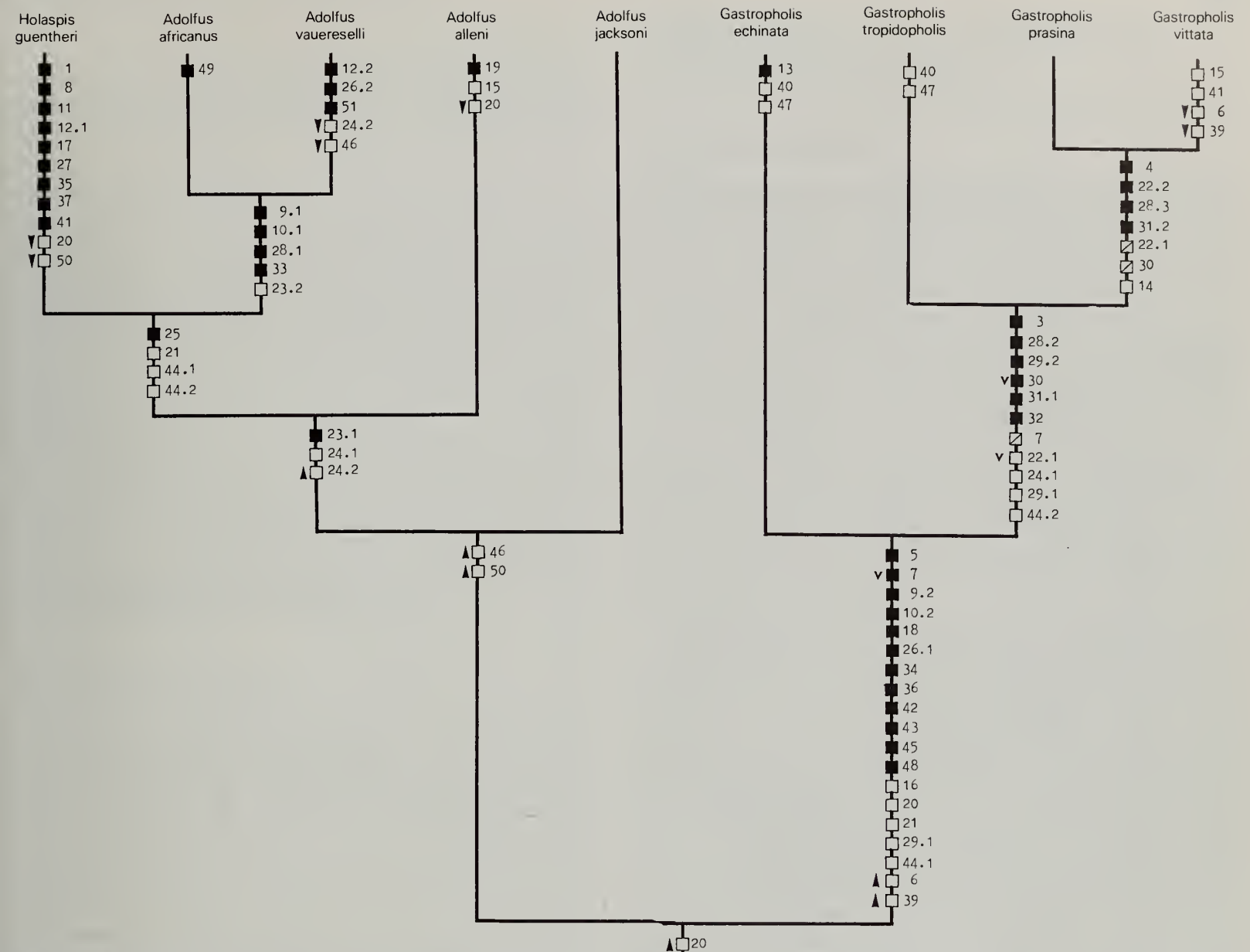


Fig. 25 Relationships of Equatorial African clade. Solid symbols indicate unique transformations within the clade, and open symbols those that occur twice. Upward pointers denote characters that subsequently reverse, at which point they are marked by downward pointers. Characters that are variable but later stabilise are indicated by V. Figures refer to specific characters; for details see Arnold, 1989.

the Equatorial African clade, the relationships of the unit made up of *Lacerta echinata*, *Bedriagaia* and *Gastropholis* to *Adolfus africanus* etc. and *Adolfus alleni* are variable.

As there are some parallelisms between the Equatorial African clade and the main branch, all the species of the former, except the most primitive, '*L.* *jacksoni*', were excluded, and characters which consequently had no shared derived states eliminated, namely 19, 22.2, 23, 42, 49.1, 49.2, 52, 59, 74. Parsimony analysis now produced just two trees of 146 steps and a consistency index of 0.473, but the ambiguity in the relationship of *Pedioplanis* and *Eremias* remained. *Philochortus* and its advanced relatives were also analysed separately in an attempt to resolve this problem, being run by the 'Branch and Bound' method. Additional characters without shared derived states eliminated were 1, 2.1, 4, 5.2, 7, 10.2, 11, 26.3, 27, 29, 30, 32, 45.2, 47, 54.2, 60, 63.1, 63.2, 64, 71, 75 and 81.2, reducing the data set to 48 characters. This again produced two trees, of 96 steps and a consistency of 0.5, with the same variants.

Compatibility analysis

Data for *Lacerta jayakari* etc. and the Ethiopian and advanced Saharo-Eurasian forms were reanalysed by the compatibility

method. This gave an overall randomness ratio of 0.83 and a compatible set of 24 characters resulting in the tree shown in fig. 19 b. Resolution is increased and the arrangement of taxa changed somewhat from that in Fig. 19 a. In general, the result is similar to the one produced by parsimony analysis, but with less definition. Removal of most members of the Equatorial clade and of *L. jayakari* etc., produces very little change. When the robust assemblage made up of *Philochortus* and its derived relatives are analysed separately, the randomness ratio is 1.01 and the *Eremias-Pedioplanis* anomaly is resolved, with *Pedioplanis* and *Eremias* being successive branches of the tree (Fig. 19c).

The Equatorial African clade

Both parsimony and compatibility methods discern *Gastropholis* and *Bedriagaia* as sister taxa and recognise '*Lacerta*' *echinata* as their nearest relative. Consideration of a larger data set for the Equatorial African clade (Arnold, 1989) confirms this grouping and produces a general pattern of relationships (Fig. 25).

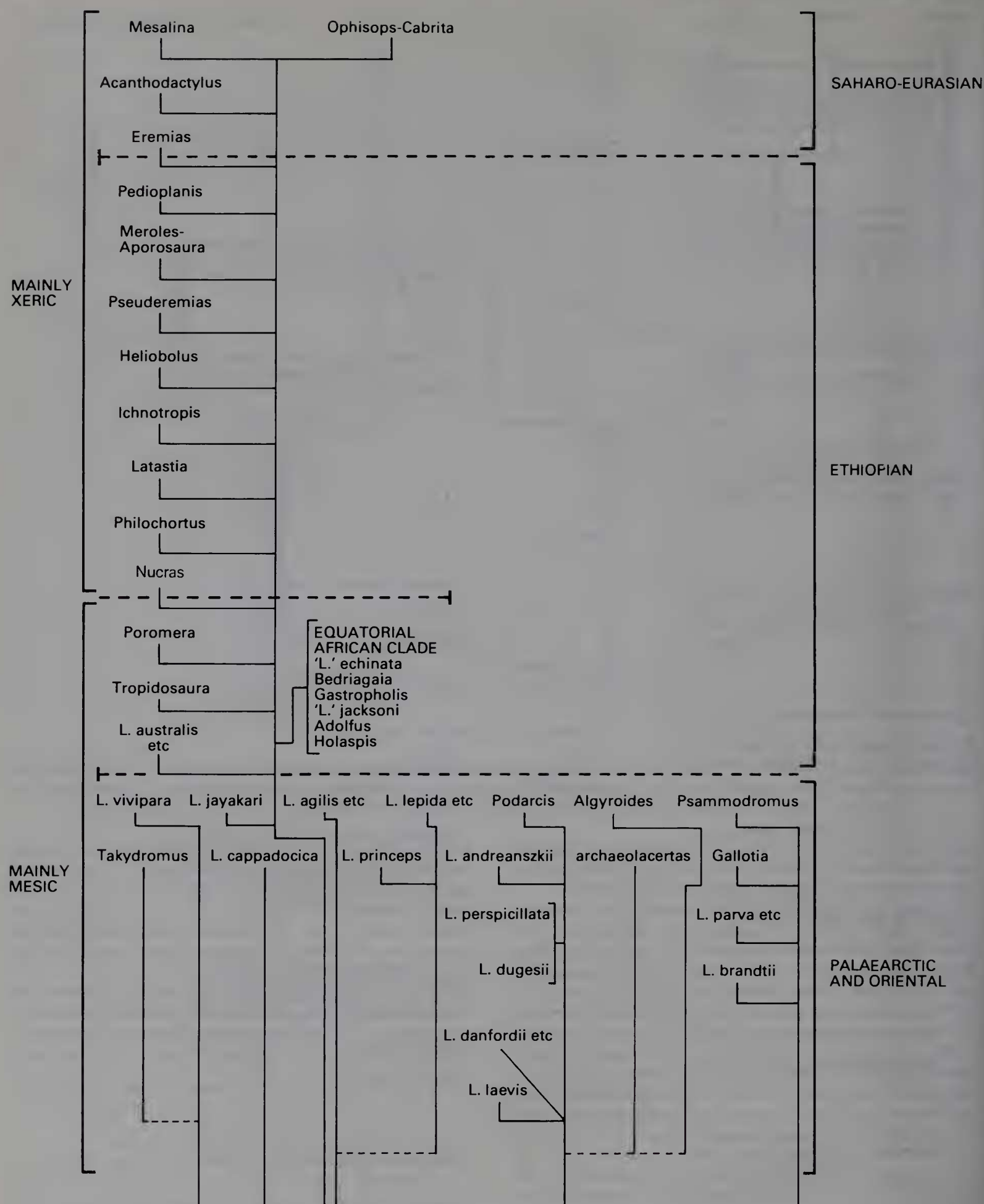


Fig. 26 Principal ecological and zoogeographic trends in the Lacertidae. Advanced taxa occur in mainly xeric habitats, while more primitive forms usually occupy quite mesic situations. The most primitive taxa are found in the Palaeartic and Oriental regions, with a group of increasingly advanced forms occupying the Ethiopian region and the most advanced occurring in the Saharan area and in the drier parts of Eurasia.

Areas of conflict

The preferred relationships of *Lacerta jayakari*, the Ethiopian species and the advanced Saharo-Eurasian forms is shown in Fig. 24. Sections where parsimony and compatibility methods differ in results or degree of resolution are discussed below.

Tropidosaura and *Poromera*.

Parsimony joins these genera as sister groups on the basis of three features involving five characters: loss of anterior frontal processes (6.1, 6.2), reduced collar (45.1, 45.2) and enlarged dorsal body scales (46). Against this, compatibility methods relate *Poromera* to more advanced forms on the strength of the dorsal process of the maxilla (5); another slightly less constant feature that also supports this relationship is the form of the fronto-parietal suture (7). Although less features support the second arrangement than the first, they are considerably less homoplasious within the Lacertidae as a whole and consequently likely to be better indicators of relationship. Given this conflict between greater number of characters on one side and perhaps better quality characters on the other, it seems best to leave the detailed relationship of *Tropidosaura* and *Poromera* unresolved.

Ichnotropis and *Heliobolus*.

Parsimony also joins these two genera as sister groups on the basis of two features and three characters: loss of anterior frontal processes (6.1, 6.2) and kidney not extending far beyond vent (65). In contrast, compatibility associates *Heliobolus* with more advanced forms on parietal width (9), although this feature also occurs in some presumably derived *Ichnotropis*. The first arrangement is supported by two instead of one binary character, but these are more homoplasious than the latter. Because of this, the relationship of *Ichnotropis* and *Heliobolus* is left undetermined.

Pedioplanis and *Eremias*.

As noted, these two genera may appear in parsimony analysis as sister groups, or *Eremias* may be associated with more advanced forms. Sister group relationship is based on large jugal exposure (16), parietal scale reaching the edge of the parietal table of skull (39.1, 39.2) and bilobed female genital sinus (79). These characters are all quite noisy, showing considerable homoplasy in the rest of the Lacertidae, and 16 and 79 are also reversals. Features associating *Eremias* with more advanced taxa than *Pedioplanis* are squamosal-parietal separation (13), shape of squamosal (14), number of chin shields (44) and hemipenial micro-ornamentation (78.2). All these are reversals, and 44 and 78.2 have numerous homoplasies elsewhere in the Lacertidae, but 13 and 14 have none. These latter two characters perform better in 'boil down' than the set supporting sister group relationship, when all Ethiopian and advanced Saharo-Eurasian forms are considered, and appear in the compatible set when just *Philochortus* and its advanced relatives are subjected to compatibility analysis. Given the greater apparent stability of characters 13 and 14, the relationship they support is preferred here.

BIOGEOGRAPHICAL ASPECTS OF LACERTID PHYLOGENY

The general pattern

The phylogeny proposed here exhibits broad geographical regularity (fig. 26). 1. The most primitive lacertid genera are found in relatively mesic habitats in the Palaearctic and Oriental regions, where the majority are restricted to the west. 2. A series of increasingly more advanced forms occupies the Ethiopian region (i.e. Africa south of the Sahara, also called the Afrotropical or Africotropical—Udvardy, 1975) with the more derived occurring in arid situations. 3. Finally, *Eremias*, *Acanthodactylus*, *Mesalina* and *Ophisops-Cabrita*, which originated from the latter, occur in and around the deserts of the North Africa and Eurasia, and in the Indian subcontinent. A simple explanation of this pattern would be that modern lacertids arose in Eurasia, invaded Africa and the Ethiopian region, evolved more xeric forms in the latter area, and then one or more derivatives of these re-entered the dry areas of Eurasia and North Africa and radiated.

The presence of the majority of the generally primitive lacertids, and indeed the most primitive modern forms, in Europe indicates the family may well have originated there, which is also supported by their long, if fragmentary, fossil history in the area, extending back at least as far as the Palaeocene (Estes, 1983a). Albumin immunology suggests that the ancestors of many modern western Palaearctic lacertids may have undergone quite rapid multiple divergence, perhaps during the early Miocene, a time when the European land-mass was very dissected, something which would have facilitated differentiation (Lutz, Bischoff & Mayer, 1986). The immunological information implies that *Lacerta jayakari* may have separated from the other Palaearctic lacertids investigated about 17-20 million years ago. This species, together with its close relative, *L. cyanura*, appears to be the sister group of the whole Ethiopian and advanced Saharo-Eurasian clade so, if the immunological date is accepted, the latter very large and diverse assemblage must have originated subsequently.

Representatives of a number of separate lacertid stocks occur in Africa and the associated Arabian area, including *Lacerta lepida* etc., members of the *Psammmodromus-Gallotia* assemblage, some species of *Podarcis* and its apparent relatives, *L. jayakari* etc. and, of course, the associated Ethiopian and advanced Saharo-Eurasian clade. All except the last unit are presently confined to the northern, Palaearctic periphery of the African-Arabian plate. The times of arrival of these various groups is unknown, but it should have been possible for lacertids to reach the area easily from some time around the closure of the Tethys sea which previously separated it from Eurasia. The date for the principle closure is estimated to be mid-Burdigalian, around 17 million years ago, when Arabia contacted the Turkish plate. Temporary connexion may also have occurred earlier in the Aquitanian (Adams, Gentry & Whybrow, 1983; Whybrow, 1984) and there may have been a brief interruption of land contact during the Langhian transgression around 16 million years ago (Steininger, Rabeder & Rögl, 1985). The Burdigalian was a time of

faunal interchange among mammals between Eurasia and Africa. By the middle of this stage, proboscideans and creodonts of African origin were in Europe and Eurasian carnivores in Africa (Steininger, Rabeder & Rögl, 1985). Among reptiles, a representative of the apparently African chameleons had reached central Europe by the Ottnangian (= upper Burdigalian) (Roček, 1984), so some lacertids might have entered Africa by then. The immunological date for the separation of *Lacerta jayakari* and consequently of the Ethiopian clade fits rather well with this. Any lacertids entering Africa through most of the Miocene are likely to have arrived via Arabia, for the proximity of Africa and Europe at the western end of the Mediterranean did not occur until the end of this period. Interestingly, the range of *L. jayakari* etc is the closest of any members of the primitive Palaeartic lacertids to the Ethiopian region by this route. Whenever the ancestors of Ethiopian lacertids entered Africa, the date when advanced xeric forms derived from them spread north into the arid regions of Eurasia and Northern Africa must inevitably have been considerably later.

Estes (1983b) suggested that the lacertids may have arisen on one of the islands that constituted Europe during the Jurassic, undergoing vicariance from a North American stock which was ancestral to teiid lizards. Presumably, these early lacertids would have given rise to the ones that appear to have existed in the European area throughout the Cenozoic. Estes thought that the more advanced African forms might have differentiated from the European ones on the island that constituted Northwest Africa in the Cretaceous. But, as we have seen, immunology suggests a much later date for the origin of the Ethiopian and advanced Saharo-Eurasian clade, and also for some groups that now occur in North Africa. An alternative version of events discussed by this author is that lacertoids were a Gondwanaland element which split into lacertid and teiid precursors with the separation of Africa and South America in the Cretaceous period. Presumably this would have been followed by Europe being invaded by primitive forms, which have persisted with relatively little change until the present day, and by such forms becoming extinct in Africa.

The various hypotheses that have been proposed for the gross historical biogeography of the Lacertidae are open to testing. Evolutionary clocks, based on immunology, amino-acid substitution in proteins or base substitution in DNA, may give a better idea of when the Ethiopian and advanced Saharo-Eurasian clade arose and when the xeric Saharo-Eurasian section of this separated. Regrettably, there is as yet no lacertid fossil record known in Africa south of the Sahara and virtually no material from the north of the continent either (Estes, 1983a), but discovery of suitable deposits may throw light on possible dates of arrival. Whether, the invasion of more northern areas by advanced xeric forms was indeed a relatively late event might also be tested by fossil evidence.

Primitive Palaeartic and Oriental forms

It is not possible to work out the overall historical biogeography of this assemblage, partly because the phylogeny is incomplete in some areas and uncertain in others. As noted, the majority of primitive lacertids are restricted to the west Palaeartic. However, one *Lacerta*, *L. vivipara*, extends eastwards to the Pacific Ocean and *Takydromus* etc. is found only in the east Palaeartic and the Oriental regions. It is not possible to be sure how the almost entirely allopatric range of

Takydromus etc. arose. If it is indeed a derivative of the paraphyletic genus *Lacerta*, its origins may lie in the European region, either its *Lacerta* ancestor migrating eastwards from this area or *Takydromus* actually evolving there. *Miolacerta* Roček, 1984, from the lower Miocene (Ottnangian) of Czechoslovakia, has tridentate lateral teeth, like *Takydromus* etc., but whether this is indicative of relationship is unknown.

A striking aspect of the distributional pattern of primitive lacertids in the western Palaeartic is the way archaeolacertas have very limited and disjunct ranges in Europe west of the Black Sea, although they are more widely distributed in Asiatic Turkey, the Caucasus and adjoining areas. In the west, they are largely restricted to high mountain massifs and it seems possible that the distributional patterns of these forms may have arisen through competition with similarly sized members of *Podarcis* which occur widely over southern Europe but not further east (Arnold, 1981b). *Podarcis* may also have restricted *Algyroides*, which again has a broken and small distribution.

Three apparent clades of primitive Palaeartic lacertids have a disjunct distribution with taxa both in southwest Asia (especially Turkey, north Iraq, northwest Iran and the Eastern seaboard of the Mediterranean) and in northwest Africa, the latter sometimes with representatives in Iberia, the Canary Islands or Madeira (Table 2). As will be seen, the same general pattern occurs in a number of other reptile taxa. Differentiation between eastern and western representatives is often very variable. In some cases forms are conspecific and disjunction may be due to recent aridification in North Africa. But in other instances, like the primitive lacertids, eastern and western sections are much more distinct and the differentiation is probably much longer standing.

Table 2 The members of some apparent clades of reptiles found in Southwest Asia and Northwest Africa

Southwest Asia	Northwest Africa etc.
Primitive Palaeartic lacertids	
1. <i>Lacerta brandtii</i> , <i>L. parva</i> etc	<i>Psammodromus</i> , <i>Gallotia</i>
2. <i>Lacerta danfordi</i> etc., <i>L. laevis</i>	<i>Lacerta andreanszkyi</i> , <i>L. dugesii</i> , <i>L. perspicillata</i> primitive <i>Podarcis</i>
3. <i>Lacerta princeps</i>	<i>Lacerta lepida</i> etc.
Other groups	
4. <i>Acanthodactylus tristrami</i> etc.	<i>Acanthodactylus erythrurus</i> etc.
5. <i>Ophisaurus apodus</i>	<i>Ophisaurus koellikeri</i>
6. <i>Blanus strauchi</i>	<i>Blanus cinereus</i>
7. <i>Vipera lebetina</i> subspp.	<i>Vipera mauretanica</i> etc.
8. <i>Mauremys caspica</i>	<i>Mauremys leprosa</i>
9. <i>Testudo g. ibera</i>	<i>Testudo g. graeca</i>

Ethiopian forms

In Africa, the more primitive forms of the Ethiopian and advanced Saharo-Eurasian clade appear to have spread widely, for the apparently most basal section, '*Lacerta*'

Table 3 Distribution of non-mesic groups of lacertids and their primitive forms in the Ethiopian region

	Distribution of group	Distribution of primitive forms
<i>Nucras</i>	Widespread, south of equatorial forest	Equatorial east
<i>Philochortus</i>	Northeast, also southern edge of Sahara with relicts further north	Northeast
<i>Latastia</i>	Northeast and east, savannah south of Sahara	Northeast
<i>Heliobolus</i>	Widespread, south of equatorial forest, also savannah north of forest	North
<i>Ichnotropis</i>	Widespread, south of equatorial forest	Equatorial east
<i>Pseuderemias</i>	Northeast	Northeast
<i>Meroles</i>	Southwest	Southwest
<i>Pedioplanis</i>	South	South

australis etc, occurs in the far south of the continent. Penetration southwards into the Ethiopian region and broad dispersal there would have been easy before the later Neogene, while conditions were widely mesic in Africa (Axelrod & Raven, 1978). In general, primitive Ethiopian taxa now have disjunct ranges, being confined to less dry areas, with *L. australis* etc. and *Tropidosaura* in various often isolated montane areas of southern Africa and *Adolfus*, *Gastropholis*, *Holaspis* and *Poromera* in the Equatorial forest region. *Nucras* and more advanced Ethiopian generic units form a sequence that occupies generally increasingly severe habitats in which aridity, high temperature and openness become more marked. This evolution may have been related to the increasing dryness of the African climate during the later Neogene (Axelrod & Raven, 1978).

Among these relatively xeric genera, most are found in the northeast and north of the drier parts of the Ethiopian region, or have their most primitive representatives there if they extend southwards (Table 3). Perhaps, this is the area where they each originated, or is at least ecologically similar. A couple of genera, *Latastia* and *Heliobolus* extend to the southern periphery of the dry areas of northern Africa and one species of *Philochortus* is more widespread there, albeit with a relict distribution. The only exceptions to the general pattern are the most advanced Ethiopian genera, *Meroles*, *Aporosaura* and *Pedioplanis*, which are now entirely confined to arid parts of southern Africa. However, these areas may well have been connected in the past with the dry northeast of the Ethiopian region (Balinsky, 1962; Seely, 1978), where *Pseuderemias*, the closest Ethiopian relative of *Meroles*, *Aporosaura* and *Pedioplanis*, is found; so these genera too may have had a northern origin. It is also possible that the precursor of advanced Saharan and Eurasian lacertids, to which *Pedioplanis* appears to be the sister group, evolved somewhere in the northern parts of the Ethiopian region.

Advanced North African and Eurasian forms

These occur mainly in dry habitats and cover an immense geographical area. Although there are only four genera, the group is very speciose with a total of about 69 species, of which 61 are members of *Eremias*, *Acanthodactylus* and

Mesalina. This compares with 54 species distributed among eight genera in the Ethiopian xeric forms. Possibly, once advanced dry-adapted lacertids arose in the Ethiopian region, they were able to enter unoccupied niche space in the Saharo-Sindian and associated central Asian desert areas, including their peripheries, and radiate there. Certainly, the dry regions where they are found do not have many other lizards that are diurnal and arid-adapted, with high heat tolerance and active hunting strategies. It is of course possible that these advanced lacertids have displaced other forms. Perhaps primitive Palaearctic taxa with some adaptation to arid conditions, such as *Psammmodromus* were once more widespread and the same may have been true of genera of Ethiopian origin that now occur only on the southern edge of the North African arid regions such as *Latastia* and *Heliobolus*, but there is no evidence of this in the form of fossils or isolated relict populations.

Although originally adapted to dry conditions, some members of the advanced Saharo-Eurasian clade show a tendency to enter rather more mesic habitats. This is especially true of *Ophisops-Cabrita* which does not penetrate into very dry areas, but the trend is also apparent in the *erythrurus* and *guineensis* species groups of *Acanthodactylus* in northwest and west Africa and, to a lesser extent, probably in sections of *Eremias* and *Mesalina* in Asia as well.

Advanced Saharo-Eurasian lacertids show some vicariance. *Eremias* is essentially confined to the Palaearctic deserts of central Asia and its environs, while the ecologically similar *Acanthodactylus*, and *Mesalina* occur mainly further south in Asia and into North Africa. As noted, *Ophisops-Cabrita* is the only generic group of lacertids to extend far into the Indian subcontinent.

One striking aspect of the distribution of advanced Saharo-Eurasian lacertids is that, although the arid region of North Africa is a very large part of their total range, it has a relatively sparse representation of these forms, in terms of species numbers. There are only fifteen endemic species present plus five more that also occur further east. This compares with about 23 in the much smaller Arabian sub-region and a total of 49 species in southwest and central Asia as a whole. Of the four genera one, *Eremias*, is entirely confined to Eurasia and, in *Acanthodactylus* and *Ophisops-Cabrita*, not only many more species occur in the east, but also more of the main branches of the phylogenies of these groups. Although less marked, this is also true of *Mesalina*.

The pattern is not restricted to lacertids, being repeated in a number of other reptile groups, including *Agama* (*Trapelus*), *Uromastix*, *Stenodactylus*, *Scincus*, and *Lytorhynchus*. These forms make up a very substantial proportion of the Saharan herpetofauna and the number of taxa that have species in the Sahara but not further east is small, the main groups being *Scincopus*, *Sphenops* and some species of *Tarentola*. In these cases, the desert forms appear to be derived from stocks in adjoining more mesic areas of Africa, respectively the *Eumeces schneideri* group, *Chalcides* and more primitive members of *Tarentola*. The low level of endemism found in the Sahara suggests that, although it is by far the largest desert in the world at the present time, most stocks occurring there now have had a longer continuous history in the east. Possibly, but by no means certainly, Asia was colonised by advanced lacertids before northern Africa. A land-bridge existed between the Horn of Africa and southern Arabia until the early Pliocene, which would have made this possible, and direct connection between Arabia and North Africa developed

soon after it was interrupted (Whybrow, 1984). The relationships of the Saharan reptile fauna will be discussed more fully elsewhere.

MAIN ECOLOGICAL AND MORPHOLOGICAL TRENDS IN LACERTID PHYLOGENY

Shift from mesic to xeric habitats

The most obvious trend in lacertid phylogeny is a shift from mesic habitats to increasingly more xeric ones (Fig. 26). This is weakly apparent in the *Gallotia*-*Psammodromus* lineage among the primitive Palaearctic forms and more obviously so in the Ethiopian and advanced Saharo-Eurasian clade. Here, *Nucras* and all its more derived relatives occur in relatively dry habitats.

Although a detailed case has not yet been made, many of the morphological changes that occur in advanced forms may well be functionally associated with the problems of survival in dry, hot environments that are often very open. A number of changes affect the snout and nasal region and could be connected with processing dry, often dusty air. Possibilities here include the large nasal opening of the skull (1), complex septomaxilla (2.1–2.4), median depression on snout (3.1–3.2), lower postnasal contacting the rostral (34), thickened postnasal area (62.1–62.2) and often complex nasal passage (63.1–63.4). The increase in the extent of the anterior kidney (64) may be related to reduction in available water, and keeled subdigital lamellae (55) appear to be important in reducing heat uptake from the ground (Arnold, 1973).

Open habitats presumably increase viewing distances which is likely to place a premium on visual acuity and be responsible for the development of the large eyes typical of these advanced forms. This in turn results in narrowing of the frontal area, perhaps making it less strong, and the fusion of the frontal bones (4) may counteract this. The more complex frontal interdigitation with the bones of the snout (5) could also increase strength. The general lightening of the skull in advanced forms, such as the reduction in osteoderms (11), may again be connected with open habitats, which might be responsible for postcranial changes as well, in particular shift from generally long, sinuous bodies with short limbs to shorter torsoes with longer legs. Perhaps associated with this is the remodelling of the thoracic region, with more widely separated xiphisternal cartilages (27), and increase in the number of short dorsal ribs (29). Another series of changes involves the back of the head, including a simpler fronto-parietal suture (7), shorter posterior cranial segment (8, 9) and loss of the quadratojugal process, perhaps all connected with greater skull mobility.

Parallelism in ecological niche and its role in character homoplasy

As might be expected in a family with a very large range, quite different lineages have entered very similar niches in different places. This has resulted in considerable character parallelism, since similar morphological adaptations are often elicited. For instance, habitual use of narrow crevices, particularly in rocks, occurs in some archaelacertas, *Podarcis*,

L. cyanura and *Holaspis* and produces a whole suite of characters (Arnold, 1973). Forms adapted to forest floor and forest edge habitats occur in *Adolfus*, *Algyroides* and among primitive *Takydromus*, while other *Takydromus* and *Poromera* specialise in climbing and running through long grassy vegetation, producing parallels in such features as elongate, slender habitus, enlarged mid-dorsals (46), weak collar (45.2) and pointed, keeled ventrals (49.2). A number of genera have entered habitats with low, dense, coarse and sometimes spiny vegetation and have developed rather stream-lined body forms and modifications that improve protection from mechanical damage (Arnold, 1973), such as collar reduction (45.2, 45.3) and large dorsal and lateral scales (46, 47) that are keeled, lanceolate and strongly overlapping. Among these are *Psammodromus*, *Adolfus alleni*, and members of *Tropidosaura*, *Ichnotropis* and *Ophisops-Cabrita*. Three different stocks, *Meroles-Aporosaura*, *Acanthodactylus* and *Eremias*, have invaded soft sand habitats and produced many parallels in such features as lateral scale rows on the fingers and toes that form supporting fringes (53.1–53.2, 54.1–54.2). Finally, large size has arisen independently in *Gallotia*, *Lacerta jayakari*, *Lacerta lepida* and its close relatives, and in the *Lacerta agilis* group. These parallelisms in niche are responsible for a proportion of the many homoplasies in the lacertid data set. In contrast, where lacertids have entered a distinctive niche or larger area of niche space only once, a number of unique states often arises, for instance in the gliding forest lacertid *Holaspis* and in the clade made up of '*Lacerta*' *echinata*, *Bedriagaia* and *Gastropholis* which occurs in specialised forest niches (Arnold, 1989).

Niche differentiation and the varying quality of morphological phylogenies in different groups

In some sections of the Lacertidae, ecological differentiation is rather subtle, for instance in *Podarcis* and many members of *Lacerta* in southern Europe and neighbouring areas (Arnold, 1987). Species differ in fairly modest aspects of spatial niche and in relatively small-scale climatic parameters, and there is evidence of considerable ecological parallelism. As might be expected from this, morphological variations tend to fairly restricted and homoplasious, and reconstruction of phylogeny is often difficult. In contrast, assemblages like *Meroles-Aporosaura* which show clear and striking niche differentiation are morphologically diverse without much homoplasy and relationships are much easier to discern.

Resemblances between advanced lacertids and macroteiids

A number of characters that occur in advanced lacertids are common in macroteiid lizards, or are paralleled by analogous states. They are absent from most primitive lacertids and the greatest proportion is found in advanced Saharo-Eurasian forms like *Acanthodactylus*. Among these features are a large nasal opening to the skull (1), a complex septomaxilla (2), fused frontal bones (4), relatively simple fronto-parietal suture (7), posterior extension of parietal bone near mid-line not extensive (11), absence of a quadratojugal process (15), large exposure of the anterior part of the jugal bone (16), no marked sexual variation in the number of presacral vertebrae (28, among advanced lacertids present in a few *Acanthodactylus* species only), anterior autotomic vertebrae with two

pairs of diverging transverse processes (31.3), more than two rows of scales on digits (53, 54), subdigital lamellae keeled (55), tongue often pale (61), anterior section of kidney expanded (64, see Cope, 1900, for teiids), m. retractor lateralis anterior inserting laterally in front of vent (66), course of ulnar nerve 'varanide' (81.2). As already noted, the lacertids that possess a high proportion of these features are usually found in relatively xeric habitats. This is also true of many macroteiids. So there may possibly be a functional basis for some of these parallelisms.

Skull characters and ontogeny

Many features of the skulls of most advanced lacertids are similar to states often found in juveniles of some more primitive forms. Amongst these are a large nasal opening (1), narrow interorbital area, simple fronto-parietal suture (7), short, broad parietal area (8,9), restricted cranial osteoderms (11) often including the supraocular ossification, and reduced quadratojugal process (15). These apparently pedomorphic features, where development has been retarded, occur alongside others where ontogenetic change extends further than is usual in primitive taxa (acceleration). This is true for instance of frontal fusion (4) and, where it occurs, fusion of the postfrontal and postorbital bones (12). Heterochronic change of this kind, where new adult features develop by phylogenetic changes in the relative timing of developmental events, appears to be a common source of evolutionary change in reptiles.

NOMENCLATURE

Binomial nomenclature attempts to fulfill two often irreconcilable purposes: firstly, to provide species with a unique and stable name, so that they can easily be referred to and information concerning them readily located; secondly, to give some idea of the relationships of species through their generic allocation (ideally, genera should be holophyletic groups). Difficulties inevitably arise when views on relationships and generic assignment change, resulting in alteration in species names. Such changes, of course, produce few problems for taxonomists or specialists in the assemblage concerned, but they are confusing for most other biologists and laymen, who may constitute the majority of users of the names. As things stand, all that can be done to ameliorate the problem is to alter generic allocation only when the evidence for such a change is very strong, and to take likely inconvenience into account before doing so. Obviously, far less trouble is caused when an obscure species rarely mentioned in the literature has its name altered than when the same thing occurs to a very well known one.

Ophisops Ménétriés, 1832 and Cabríta Gray, 1938

These nominal genera share a wide range of derived features, including the presence of an extremely large, transparent 'window' in the lower eyelid which, in this extreme form, is found nowhere else within the Lacertidae. There can be no doubt that they constitute a holophyletic group and *Cabríta* is distinguished from *Ophisops* only by its eyelids not being completely fused together as they are in the latter. This is a

primitive condition and cannot be used to define a holophyletic group. Moreover, the two species that constitute *Cabríta* are each more closely related to particular species of *Ophisops* than they are to each other. *Cabríta jerdonii* Beddome, 1870 is allied to *Ophisops jerdoni* Blyth, 1853 and *Ophisops beddomii* (Jerdon, 1870), while the relationships of *Cabríta leschenaultii* (Milne-Edwardes, 1829) lie with *Ophisops microlepis* Blanford, 1870. Therefore, *Cabríta* cannot be regarded as a separate genus and is relegated to the synonymy of *Ophisops*. As *Cabríta jerdonii* shares a trivial name with a species already in *Ophisops*, and acquired it later, a new one is necessary. I propose *Ophisops nictans*, the name meaning 'blinking', in reference to the ability of this species to open and close the eyes, unlike most of its congeners.

Meroles Gray, 1838 and Aporosaura Boulenger, 1887

As argued elsewhere (Arnold, in press), there is good evidence that *Aporosaura anchietae* is the sister group of a clade made up of three advanced species of *Meroles*, namely *M. ctenodactylus* (A. Smith, 1838), *M. cuneirostris* (Strauch, 1867) and *M. micropholidotus* (Mertens, 1938). Continuing to exclude the monotypic genus *Aporosaura* from *Meroles* would consequently make the latter paraphyletic. Furthermore, many of the distinctive features of *Aporosaura* are clearly foreshadowed in advanced *Meroles*, and for these two reasons I propose to transfer it to this genus. It is regrettable in many ways to alter a binomial which has stood for over a century, but such a change would reflect the clearly established relationships of the species, and may not cause too much inconvenience as usages of the name *Aporosaura anchietae* have been quite restricted. Also, the fact that the species has a distinctive trivial name within the Lacertidae makes confusion less likely.

Equatorial African lacertids

The nomenclature of these forms is discussed elsewhere (Arnold, 1989). Briefly, *Gastropholis*, *Bedriagaia* and 'L.' *echinata* form a very well defined clade and are all placed in the first genus. 'L.' *jacksoni* is clearly more closely related to other members of the Equatorial African group of lacertids than it is to any Palearctic *Lacerta*, and consequently needs to be reallocated. While the most plesiomorphic member of the total Equatorial African clade, 'L.' *jacksoni* is, on balance, more likely to be related to *Adolfus* than to *Gastropholis* in its new sense and is consequently transferred to the former. *Holaspis guentheri* raises potential difficulties. It is morphologically very distinct and has many autapomorphies, but may well be the sister taxon of *Adolfus africanus* and *A. vauereselli*. Leaving it as a monophyletic genus could consequently make *Adolfus* paraphyletic. However, if *Holaspis* and *Adolfus* were merged, the law of priority would demand that the four species of *Adolfus* were transferred to *Holaspis*, with consequent name changes, and the great distinctiveness of *Holaspis guentheri* would cease to be emphasised. More worryingly, the case for regarding *Holaspis* as sister taxon of two of the species of *Adolfus* is not entirely conclusive, so there is a risk that further taxonomic changes are possible. For these reasons, I think it is best to retain *Holaspis* as a monotypic genus and leave *Adolfus*, which is rather poorly defined, as probably paraphyletic for the present. Paraphyly could be avoided by splitting *Adolfus*, confining the name to the type species *A. africanus* and to *A. vauereselli*, and giving separate

generic allocations to *alleni* and *jacksoni*. But such a course would create new names, separate generally similar forms and may not be permanent since the relationships of these species are yet to be very strongly substantiated.

***Takydromus* Daudin, 1802 and *Platyplacopus* Boulenger, 1917**

Boulenger (1917) separated *Platyplacopus* from *Takydromus* on the basis of the structure of the digits. Examination of the members of both nominal genera, shows considerable variation in this feature and it is not possible to delineate the two taxa clearly. Furthermore, separation of *Platyplacopus* appears to make *Takydromus* paraphyletic. The species of *Platyplacopus* are consequently returned to *Takydromus*.

Podarcis

For a long time, *Podarcis* was treated as a subgenus of *Lacerta* (e.g. Boulenger, 1916) but was subsequently raised to full generic status (Arnold, 1973). As understood here, it is made up of fifteen species which share a number of derived features and, although none of these are unique, there is little doubt that the group is holophyletic. Moreover, its members are very alike morphologically, have a close biochemical resemblance (p. 235) and are also relatively similar in many aspects of their ecology and biogeography. This general uniformity means that they are often referred to collectively and it is therefore convenient to have a distinct name for them and to reflect their relationship in their binomials, especially as the separation of *Podarcis* is now generally accepted.

Böhme (1984, 1986) has reviewed in some detail the merits of removing *Podarcis* from *Lacerta*. While continuing to recognise it as separate, he notes that some of its distinctive features also occur among members of the genus *Lacerta*, which are superficially similar, and also in *Psammotromus* and *Gallotia*. There are eleven probably derived features of *Podarcis*, as defined above: jugal bone stepped (17), sternal fontanelle heart-shaped (26.2), anterior autotomic caudal vertebrae C-type (31.3), postnasal scale single (32), parietal scale extending to anterior edge of parietal table (39.2), first supratemporal scale often narrow (st), strong sexual dichromatism (sd), hemipenis with long lobes (72), hemipenis with large lips (73), hemipenial micro-ornamentation of recurved spines (78.2), oviducts entering genital sinus at its tips (80). Among other primitive western Palaearctic lacertids that have more than one or two of them, the features are distributed in the following way (ones that are not universal or present in a rather different form in *Podarcis* are placed in parentheses). *Lacerta andreanskyi*—32, 39.2, 73, 78.2, st; *L. perspicillata*—39.2, 73, 78.2, st; *L. dugesii*—39.2, (78.2), st, (sd); *L. danfordi*—31.3, 72, 73; *L. vivipara*—32, 39.2, (sd); *Psammotromus*—31.3, 32, 39.2, 72, 73, 78.2, 81.2; *Gallotia*—31.3, 32, (39.2), 72, 78.2, (st) (sd) Resemblance between *Podarcis* and *Psammotromus* and *Gallotia* is relatively strong, but these groups have distinctive features of their own and their relationships certainly appear to lie elsewhere. In the case of the species of *Lacerta*, none shares more than a small proportion of the distinctive features of *Podarcis*, so there is consequently a good case for recognizing the latter as a separate entity.

As noted (p. 235), Richter (1980) recognised *Lacerta dugesii* and *Lacerta perspicillata* as being closely related and made them the sister group of *Podarcis* as understood above.

He regarded the two units as subgenera, *Teira* and *Podarcis* s. str. and included them both in an expanded genus *Podarcis* s. lat., a course that was followed by Böhme (1984, 1986). In fact, as we have seen, *Lacerta dugesii* and *L. perspicillata* possess only a small proportion of the distinctive features of *Podarcis* in its narrow sense and their inclusion consequently dilutes a very uniform group. My inclination would be to exclude them from the genus.

Primitive Palaearctic genera and the problem of *Lacerta*

Most genera within the primitive Palaearctic assemblage are clearly holophyletic and well defined. These include the long-established *Algyroides* and *Psammotromus*, *Takydromus* (as defined above), *Podarcis* and *Gallotia*, which like *Podarcis* was long regarded as a subgenus of *Lacerta* (Boulenger, 1916) but subsequently raised to full generic status (Arnold, 1973). All these taxa are now generally accepted, leaving the other primitive western Palaearctic forms as a single genus, *Lacerta* s. lat. This is undoubtedly paraphyletic, for advanced Ethiopian and Saharo-Eurasian lacertids and all or most of the genera listed at the beginning of this section appear to have arisen from within it. Ideally therefore, in terms of expressing relationship, *Lacerta* s. lat. should be broken up into holophyletic units, attaching species if necessary to taxa which have sprung from it. Regrettably, such a course is not easy. As we have seen, some species could be attached to *Podarcis* by expanding it, and the same could be done in some other instances. But, elsewhere, relationships within *Lacerta* s. lat. are rarely known with any certainty so that the supposed holophyletic groups produced are likely to be of doubtful validity or very small. To give all these generic status would make for instability and split *Lacerta* s. lat. into many fragments. It seems better, for the present, to accept *Lacerta* s. lat. as an admittedly paraphyletic assemblage confined to the Palaearctic region and employ subgenera within it if supposed relationship is to be formally emphasised. A number of suitable names are already in use: *Apathya* Méhely, 1909 (Type species: *Lacerta cappadocica*); *Archaeolacerta* Mertens, 1921 (Type species: *Lacerta bedriagae*); *Lacerta*, Linnaeus, 1758 s. str. (Type species: *Lacerta agilis*); *Omanosaura* Lutz, Bischoff & Mayer, 1986 (Type species: *Lacerta jayakari*); *Teira* Gray, 1845 (Type species: *Lacerta dugesii*); *Thimon* Tschudi, 1836 (Type species: *Lacerta lepida*); *Zootoca* Wagler, 1830 (Type species: *Lacerta vivipara*).

'*Lacerta australis*' and '*Lacerta*' *rupicola*

These two South African species have ranges very distant from the rest of *Lacerta* s. lat., especially when the Equatorial African forms once assigned to the genus have been reallocated. Also the South African species share a number of features with other Ethiopian lacertids which are not found in the apparent closest Palaearctic relatives, namely *Lacerta jayakari* etc. They consequently deserve separate generic status and I propose the name *Australolacerta* for them with the type species *Lacerta australis* Hewitt, 1926.

Suggested divisions of the Lacertidae

Two suggestions have recently been made that would divide the Lacertidae. But, as argued previously (Böhme, 1981; Böhme, Hutterer & Bings, 1985) both should be rejected. Shcherbak (1975) proposed that the subfamily Eremiinae

should be recognised for the following genera: *Lampreremias* (= *Heliobolus*), *Pseuderemias*, *Taenieremias* (now assigned to *Acanthodactylus*), *Mesalina* (= *Mesalina* and *Pedioplanis*), *Meroles* and *Eremias*. This taxon would be paraphyletic, since *Ophisops* (including *Cabrita*) and most species of *Acanthodactylus* would be excluded. The recognition of the Eremianinae would also make the rest of the Lacertidae paraphyletic and divide the family in an arbitrary manner. Cano, Baez, Lopez-Jurado & Ortega (1984) suggested that *Gallotia* should be placed in a separate family, the Gallotiidae, on the grounds that the genus has a distinctive karyology, but the difference involved is relatively trivial and *Gallotia* is no more distinctive than many other lacertid genera. As with Eremianinae, the recognition of Gallotiidae would make the rest of the Lacertidae paraphyletic.

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APPENDIX 1

Evidence for polarity of characters.

The following indicators of polarity are used.

1. Outgroup indicators
 - a. State widespread in tetrapods or at least lizards.
 - b. State universal or nearly so in scincomorphs apart from lacertids.
 - c. State found in majority of scincomorphs apart from lacertids.
 - d. State present in primitive members of scincomorph families, apart from lacertids.
 2. Outgroup criterion within studied group.
 3. Ontogeny.
 4. Overall commonality: present in over 80% of taxa; brackets indicate present in less than 80% but more than 50% of taxa.
 5. Universal or common state in primitive Palaeartic forms.
 6. Polarity indicated by tree of African and advanced lacertids produced by compatibility analysis.
 7. Polarity indicated by tree of Psammmodromus and its relatives produced by compatibility analysis.
- * indicates characters with good polarity evidence from other sources used to orientate trees produced from compatibility analysis.

Primitive state of character	Polarity indicators										
	1a	1b	1c	1d	2	3	4	5	6	7	
1. Nasal opening of skull small	1		+			–	(+)	+	+		
2. Septomaxilla simple	2			+			(+)	+	+		
3. Medial depression on snout absent	3	+					(+)	+	*		
4. Frontal bones unfused	4	+		+		+	(+)	+	*		
5. Dorsal process of maxilla unembraced	5		+				(+)	+	*		
6. Anterior descending frontal processes present	6	+	+		+		+	+			
7. Fronto-parietal suture complex	7		–			–		+	+		
8. Osteodermal area of parietal bone relatively long	8	unsurveyed					(+)	+	+		
9. Osteodermal area of parietal bone relatively narrow	9	unsurveyed					(+)	+	+		
10. Pineal fontanelle present	10	+	+			(+)	+	+	*		
11. Cranial osteoderms to back of parietal bone	11		–			–		+	*		
12. Postorbital and postfrontal bones unfused	12	+				+	(+)	+			
13. Squamosal-parietal contact absent	13		+					+	+		
14. Squamosal bone shallow	14		+					+	+		
15. Quadratojugal process distinct	15						(+)	+	+		
16. Lateral exposure of anterior jugal small	16		+				(+)	+	+		
17. Lower border of jugal unstepped	17	+					+	+			
18. Inner crest of jugal visible behind ectopterygoid	18		+				+	+		*	
19. Ossification of temporal scales absent	19		+			+	+	+	+		
20. Lateral teeth with one or two cusps	20		+		+		+	+			
21. Radial portion of scleral ossicle 14 present	21	+					+	+	+		
22. Continuity of clavicle loop varying intraspecifically	22		–			+	(–)	+	+	+	
23. Medial expansion of clavicle large	23		+				+	+			
24. Arms of interclavicle not directed backwards	24		+				+	+			

Primitive state of character		Polarity indicators									
		1a	1b	1c	1d	2	3	4	5	6	7
25. Interclavicle unflanged	25			+				+	+		
26. Sternal fontanelle large and elliptical	26			-		+	+	+	+	+	
27. Xiphisternal cartilages close together	27		(+)					(+)	+	*	
28. Sexual variation in number of presacral vertebrae	28	-	-			+		+	+	+	+
29. Few short free dorsal ribs	29								+	+	
30. Inscriptional ribs often present	30			+					+	+	
31. Both A and B pattern caudal processes present	31		-					-	+	+	
32. Postnasal scales two	32			-				+		+	+
33. Postnasal and supranasal separated beneath nostril	33			+				(+)	+	+	
34. Lower postnasal not contacting rostral	34		+					(+)	+	*	
35. Supranasal not contacting loreal	35	both widespread						+	+		
36. Extended lower postnasal not divided	36			(+)		+		+	+		
37. Rostral scale wide	37	unsurveyed				+		+	+	+	
38. Second supraciliary scale not elongate	38	+	+			+		+	+	+	
39. Lateral border of parietal scale within edge of table	39			+		+			+		
40. Occipital normal	40			(+)		+		+	+		
41. Interparietal normal	41			-		+		+	+		
42. No window in lower eyelid	42			+		+		+	+	+	
43. Masseteric scale present	43		-					-?	+		+
44. Five chin shields	44			+				+	+		
45. Collar well developed with granules beneath	45							+	+	+	+
46. Mid-dorsal body scales small	46							+	+	+	?
47. Lateral body scales small	47							+	+	+	
48. Six or eight longitudinal rows of ventral scales	48			+	+	+		(+)	+	+	

Primitive state of character		Polarity indicators									
		1a	1b	1c	1d	2	3	4	5	6	7
49. No keeling on ventral scales	49		+					+	+	*	
50. Ventral scales in straight longitudinal rows	50		+			+		+	+		
51. Femoral pores unreduced	51			+		+		+	+		
52. Scales bearing femoral pores flattish	52		+					+	+	+	
53. No lateral scale rows on fingers	53			+		+		+	+		
54. No lateral scale rows on toes	54			+		+		+	+		
55. Subdigital lamellae smooth	55			+				+	+	+	
56. Axillary mite pocket absent	56			+				+	+		
57. Post-femoral mite pocket absent	57			+				+	+		
58. Scales bordering ventral mid-line of tail small	58		+					+	+	+	
59. Body scale micro-ornamentation coarsely striate	59			+				+	+		
60. Outer ventrals with blue pigment	60								+		
61. Tongue predominantly dark	61			-					+		+
62. Postnasal area thin in horizontal section	62			+				+	+	+	
63. Nasal vestibule short	63			+				+	+	*	
64. Anterior kidney short	64			+				+	+	+	
65. Posterior kidney extending well beyond vent	65			+				+	+	+	
66. RLA muscle insertion near mid-line	66			-					+		
67. RLA muscle not enlarged in front of vent	67			+				+	+		
68. RLA muscle not attaching to base of hemipenis	68			+				+	+		
69. No thoracic fascia	69			+					+	+	
70. No hemipenial armature	70	+	+						+		
71. Transverse section of hemipenial lobes simple	71	+	+						+		
72. Hemipenial lobes relatively short	72								+		

Primitive state of character		Polarity indicators									
		1a	1b	1c	1d	2	3	4	5	6	7
73. Hemipenial lips moderate or small	73			+					+		
74. Hemipenial connectors not close to clavular tips	74								+		
75. Medial side of hemipenis not reduced	75	+	+			+		+	+		
76. Lateral side of hemipenis not reduced	76	+	+			+		+	+		
77. Hemipenis without large pointed papillae	77			+				+	+		*
78. Hemipenial microornamentation crown-shaped	78										+
79. Female genital sinus bilobed	79			+					+	+	
80. Oviducts exit ventrally	80								+		
81. Ulnar nerve ‘Lacertide’	81	+		+					+	*	
82. Lateral septum on bodenaponeurosis	82		+					+	+		*
83. Usually mute	83			+				+	+		*
84. Flank of female bitten in copulation	84					+		+	+	+	+

Distribution of characters used in analysis (see p. 216)

Character Nos.

V - Primitive state 1 - Derived state			— - no data.																		
			1	2.1	2.2	2.3	2.4	3.1	3.2	4	5	6.1	6.2	7	8	9	10.1	10.2	11	12	
Appendix 2 (part a)																					
	Ancestor		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Ophisops-Cabrita</u>		1	1	1	1	1	1	1	1	1	V	V	1	1	1	0	0	1	0	
	<u>Mesalina</u>		1	1	1	1	1	1	1	1	1	V	0	1	1	1	0	0	1	0	
	<u>Acanthodactylus</u>		1	1	1	0	0	1	1	1	1	V	0	1	1	1	0	0	1	V	
	<u>Eremias</u>		1	1	1	0	0	1	1	1	1	V	0	1	1	1	0	0	V	1	
	<u>Pedioplanis</u>		1	1	1	1	0	1	1	1	1	1	0	1	1	1	0	0	1	V	
	<u>Meroles-Aporosaura</u>		1	1	1	0	0	V	1	1	1	0	0	1	1	1	0	0	1	1	
	<u>Pseudieremias</u>		1	1	1	0	0	1	1	1	1	0	0	1	1	1	0	0	1	0	
	<u>Heliobolus</u>		1	1	0	0	0	1	1	1	1	1	1	1	1	1	0	0	1	0	
	<u>Ichnotropis</u>		1	1	0	0	0	1	1	1	1	1	1	1	1	V	0	0	1	1	
	<u>Latastia</u>		1	1	0	0	0	1	1	1	1	0	0	1	0	0	0	0	1	0	
	<u>Philochortus</u>		1	1	0	0	0	0	0	1	1	0	0	1	0	0	1	0	1	1	
	<u>Nucras</u>		0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	
	<u>Poromera</u>		0	0	0	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	
	<u>Tropidosauria</u>		0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	
	<u>Holaspis</u>		1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	
	' <u>Lacerta</u> ' <u>australis</u> etc		0	-	-	-	-	0	0	0	-	0	0	0	0	0	0	0	0	0	
	<u>Gastropholis</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	
	<u>Bedriagaia</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	
	' <u>Lacerta</u> ' <u>echinata</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	
	<u>Adolfus alleni</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	
	<u>Adolfus africanus</u> etc		0	0	0	0	0	0	0	0	0	V	0	0	0	0	1	1	0	1	
	' <u>Lacerta</u> ' <u>jacksoni</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	
	<u>Takydromus</u> etc		0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	
	<u>Gallotia</u>		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
	<u>Psammmodromus algerus</u>		0	1	0	0	0	1	0	0	0	V	0	0	0	0	0	0	0	1	
	<u>Psamm. hispanicus</u> etc		0	1	0	0	0	1	V	0	0	V	0	0	0	0	0	0	0	1	
	<u>Lacerta parva</u> etc		0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta brandtii</u>		0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Podarcis</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta andreanszkii</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta perspicillata</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta dugesii</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta danfordi</u> etc		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta laevis</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta</u> , <u>archaeolacertas</u>		V	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta oxycephala</u>		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta graeca</u>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Algyroides</u>		V	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta cappadocica</u>		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta agilis</u> etc		0	0	0	0	0	V	0	0	0	0	0	0	0	0	0	0	0	V	
	<u>Lacerta princeps</u>		0	0	0	0	0	V	0	0	0	0	0	0	0	0	0	0	0	1	
	<u>Lacerta lepida</u> etc		0	0	0	0	0	V	0	0	0	0	0	0	0	0	0	0	0	V	
	<u>Lacerta jayakari</u> etc		V	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
	<u>Lacerta vivipara</u>		0	0	0	0	0	0	0	0	0	V	0	0	0	0	0	0	0	1	
	Hypo. Ethiopian ancestor		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Appendix 2 (part b)

	13	14	15	16	17	18	19	20	21	22.1	22.2	23	24	25	26.1	26.2	26.3	27
Ancestor	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Ophisops-Cabrita</u>	0	0	V	1	0	0	0	0	0	0	1	0	0	V	1	1	0	1
<u>Mesalina</u>	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1
<u>Acanthodactylus</u>	0	0	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	1
<u>Eremias</u>	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1
<u>Pedioplanis</u>	1	1	1	V	0	0	0	0	0	0	1	0	0	0	1	1	0	1
<u>Meroles-Aporosaura</u>	1	1	0	1	0	0	0	0	1	0	1	0	0	0	V	V	V	1
<u>Pseudieremias</u>	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<u>Heliobolus</u>	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<u>Ichnotropis</u>	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1
<u>Latastia</u>	1	1	0	V	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<u>Philochortus</u>	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1
<u>Nucras</u>	1	0	0	0	0	0	0	0	0	0	1	V	0	0	0	0	0	0
<u>Poromera</u>	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0
<u>Tropidosaura</u>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<u>Holaspis</u>	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	0
' <u>Lacerta</u> ' <u>australis</u> etc	0	0	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	0
<u>Gastropholis</u>	V	V	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<u>Bedriagaia</u>	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0
' <u>Lacerta</u> ' <u>echinata</u>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<u>Adolfus alleni</u>	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0
<u>Adolfus africanus</u> etc	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
' <u>Lacerta</u> ' <u>jacksoni</u>	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<u>Takydromus</u> etc	V	V	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0
<u>Gallotia</u>	0	0	0	0	0	0	V	V	0	0	1	0	0	0	0	0	0	0
<u>Psammodromus algirus</u>	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0
<u>Psamm. hispanicus</u> etc	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
<u>Lacerta parva</u> etc	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<u>Lacerta brandtii</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Podarcis</u>	0	0	0	0	1	0	V	0	0	V	0	0	0	0	1	1	0	0
<u>Lacerta andreanszkii</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<u>Lacerta perspicillata</u>	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
<u>Lacerta dugesii</u>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<u>Lacerta danfordi</u> etc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<u>Lacerta laevis</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<u>Lacerta, archaeolacertas</u>	0	0	0	0	0	0	0	0	0	V	0	0	0	0	0	0	0	0
<u>Lacerta oxycephala</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Lacerta graeca</u>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<u>Algyroides</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	V	0	0	0
<u>Lacerta cappadocica</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Lacerta agilis</u> etc	0	0	0	0	1	0	V	0	0	0	0	0	0	0	0	0	0	0
<u>Lacerta princeps</u>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<u>Lacerta lepida</u> etc	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<u>Lacerta jayakari</u> etc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Lacerta vivipara</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hypo. Ethiopian ancestor	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0

Appendix 2 (part c)

	28	29	30	31.1	31.2	31.3	32	33	34	35	36	37	38	39.1	39.2	40.1	40.2	41.1
<u>Ancestor</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Ophisops-Cabrita</u>	0	1	1	0	1	1	0	1	1	0	V	0	V	0	0	0	0	0
<u>Mesalina</u>	0	0	1	0	1	1	0	1	1	0	0	0	0	1	1	0	V	V
<u>Acanthodactylus</u>	V	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0
<u>Eremias</u>	0	1	1	1	0	0	0	1	1	0	0	1	0	1	1	0	1	0
<u>Pedioplanis</u>	0	1	1	1	0	0	0	1	1	0	0	0	0	1	1	0	0	V
<u>Meroles-Aporosaura</u>	0	1	1	1	0	0	0	1	1	0	0	V	0	V	V	0	V	0
<u>Pseudieremias</u>	0	1	1	1	0	0	0	1	1	0	1	0	0	V	V	0	V	0
<u>Heliobolus</u>	0	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	V	0
<u>Ichnotropis</u>	0	1	1	1	0	0	0	1	1	0	0	0	V	0	0	0	V	0
<u>Latastia</u>	0	1	1	1	0	0	0	V	0	0	-	0	0	0	0	0	0	0
<u>Philochortus</u>	0	1	1	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0
<u>Nucras</u>	0	V	V	1	0	0	0	1	0	0	-	0	0	0	0	0	0	0
<u>Poromera</u>	0	V	1	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0
<u>Tropidosaura</u>	0	0	1	1	0	0	V	V	0	0	-	0	V	0	0	0	0	0
<u>Holaspis</u>	0	0	1	1	0	0	1	1	0	0	-	0	0	1	1	0	0	0
<u>'Lacerta' australis etc</u>	0	V	1	1	0	0	0	V	0	0	-	0	0	V	0	0	0	0
<u>Gastropholis</u>	0	0	0	1	0	0	1	1	0	0	-	0	0	1	1	0	0	0
<u>Bedriagaia</u>	0	0	0	1	0	0	1	0	0	0	-	0	0	1	1	0	0	0
<u>'Lacerta' echinata</u>	0	0	0	1	0	0	1	0	0	0	-	0	0	1	1	0	0	0
<u>Adolfus alleni</u>	0	0	0	1	0	0	1	0	0	0	-	0	0	1	1	0	0	0
<u>Adolfus africanus etc</u>	0	0	V	1	0	0	1	V	0	0	-	0	0	1	1	0	0	0
<u>'Lacerta' jacksoni</u>	0	0	1	1	0	0	1	0	0	0	-	0	0	1	1	0	0	0
<u>Takydromus etc</u>	0	0	V	1	0	0	V	0	0	V	-	0	V	V	0	0	0	0
<u>Gallotia</u>	1	V	V	0	1	1	1	0	0	0	-	0	0	1	V	0	0	0
<u>Psammmodromus algerus</u>	0	0	0	0	1	1	1	0	0	0	-	0	1	1	1	0	0	0
<u>Psamm. hispanicus etc</u>	0	0	0	0	1	1	1	1	0	0	-	0	1	1	1	0	0	0
<u>Lacerta parva etc</u>	0	0	1	0	1	0	V	1	0	0	-	0	0	1	0	0	0	0
<u>Lacerta brandtii</u>	0	V	1	0	1	0	0	1	0	0	-	0	0	0	0	0	0	0
<u>Podarcis</u>	0	0	V	0	1	1	1	0	0	0	-	0	0	1	1	0	0	0
<u>Lacerta andreanszkii</u>	0	0	0	0	0	0	1	0	0	1	-	0	0	1	1	0	0	0
<u>Lacerta perspicillata</u>	0	0	1	0	0	0	0	1	0	0	-	0	0	1	1	0	0	0
<u>Lacerta dugesii</u>	0	V	1	0	0	0	0	0	0	0	-	0	0	1	1	0	0	0
<u>Lacerta danfordi etc</u>	0	1	1	0	1	V	0	0	0	0	-	0	0	1	0	0	0	0
<u>Lacerta laevis</u>	0	0	1	0	0	0	0	0	0	0	-	0	0	1	0	V	0	0
<u>Lacerta, archaeolacertas</u>	0	0	V	V	0	0	V	0	0	V	-	0	0	1	V	0	0	0
<u>Lacerta oxycephala</u>	0	0	1	0	0	0	0	0	0	0	-	0	0	1	0	0	0	0
<u>Lacerta graeca</u>	0	0	1	0	0	0	0	0	0	0	-	0	0	1	0	0	0	0
<u>Algyroides</u>	0	0	1	0	0	0	V	0	0	0	-	0	0	1	V	0	0	0
<u>Lacerta cappadocica</u>	0	V	1	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0
<u>Lacerta agilis etc</u>	0	V	0	0	0	0	V	0	0	0	-	0	0	0	0	V	0	0
<u>Lacerta princeps</u>	0	V	0	0	0	0	0	0	0	0	-	0	0	0	0	V	0	0
<u>Lacerta lepida etc</u>	0	V	0	0	0	0	0	0	0	0	-	0	0	0	0	V	0	0
<u>Lacerta jayakari etc</u>	0	1	1	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0
<u>Lacerta vivipara</u>	0	0	V	1	0	0	1	0	0	1	-	0	0	1	1	0	0	0
<u>Hypo. Ethiopian ancestor</u>	0	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0

Appendix 2 (part e)

	53.2	54.2	56	58	60	62.1	63.1	63.3	64								
	54.1	55	57	59	61	62.2	63.2	63.4	65								
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Ophisops-Cabrita</u>	0	0	0	1	0	V	0	0	1	V	1	1	1	1	1	1	0
<u>Mesalina</u>	0	0	0	1	0	0	0	0	1	1	1	1	1	1	1	1	1
<u>Acanthodactylus</u>	V	1	0	1	0	V	0	0	1	1	1	1	1	1	1	1	0
<u>Eremias</u>	V	V	V	1	0	0	0	0	1	1	1	1	1	1	1	1	0
<u>Pedioplanis</u>	0	0	0	1	V	0	0	0	1	1	1	1	1	1	1	1	1
<u>Meroles-Aporosaura</u>	V	1	V	V	0	0	0	0	1	0	1	1	1	1	1	V	0
<u>Pseudieremias</u>	0	V	0	1	0	0	0	0	1	1	1	0	1	1	1	0	0
<u>Helioholus</u>	0	0	0	1	0	1	0	0	1	1	1	0	1	1	0	0	1
<u>Ichnotropis</u>	0	V	0	1	V	0	0	0	1	0	1	0	1	1	0	0	1
<u>Latastia</u>	0	0	0	1	0	V	0	0	1	1	0	0	1	1	0	0	1
<u>Philochortus</u>	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1
<u>Nucras</u>	0	0	0	0	0	V	0	0	1	1	0	0	0	0	0	0	1
<u>Poromera</u>	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
<u>Tropidosaura</u>	0	0	0	0	V	0	0	0	1	0	0	0	0	0	0	0	0
<u>Holaspis</u>	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1
' <u>Lacerta</u> ' <u>australis</u> etc	0	0	0	0	V	0	0	0	1	0	0	0	-	-	-	-	0
<u>Gastropholis</u>	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
<u>Bedriagaia</u>	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0
' <u>Lacerta</u> ' <u>echinata</u>	0	0	0	0	0	V	0	1	1	1	0	0	0	0	0	0	0
<u>Adolfus alleni</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Adolfus africanus</u> etc	0	0	0	0	0	V	0	0	1	0	0	0	0	0	0	0	0
' <u>Lacerta</u> ' <u>jacksoni</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Takydromus</u> etc	0	0	0	0	0	0	0	1	1	V	0	0	0	0	0	0	0
<u>Gallotia</u>	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0
<u>Psammmodromus algirus</u>	0	0	0	0	0	0	0	1	1	V	0	0	1	1	1	1	0
<u>Psamm. hispanicus</u> etc	0	0	0	V	0	0	0	0	1	V	0	0	1	1	1	1	0
<u>Lacerta parva</u> etc	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1
<u>Lacerta brandtii</u>	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
<u>Podarcis</u>	0	0	0	0	0	0	0	0	0	0	0	0	V	0	0	0	0
<u>Lacerta andreanszkii</u>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<u>Lacerta perspicillata</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Lacerta dugesii</u>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<u>Lacerta danfordi</u> etc	0	0	0	0	0	0	0	0	0	V	0	0	0	0	0	0	0
<u>Lacerta laevis</u>	0	0	0	0	0	V	0	0	0	0	0	0	0	0	0	0	0
<u>Lacerta, archaeolacertas</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Lacerta oxycephala</u>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<u>Lacerta graeca</u>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<u>Algyroides</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Lacerta cappadocica</u>	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1
<u>Lacerta agilis</u> etc	0	0	0	0	0	0	0	0	1	0	0	0	V	0	0	0	0
<u>Lacerta princeps</u>	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
<u>Lacerta lepida</u> etc	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0
<u>Lacerta jayakari</u> etc	0	0	0	V	0	0	0	0	1	0	0	0	0	0	0	0	0
<u>Lacerta vivipara</u>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hypo. Ethiopian ancestor	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Appendix 2 (part f)

(part f)	66	67	68	69.1	69.2	70	71	72	73	74	75	76	77	78.1	78.2	79	80	81.1
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Ophisops-Cabrila</u>	V	0	1	1	1	1	1	-	-	0	0	0	0	0	0	0	1	1
<u>Mesalina</u>	0	1	1	1	1	1	1	-	-	0	0	V	0	0	0	0	1	1
<u>Acanthodactylus</u>	1	0	0	1	1	1	V	-	-	0	V	0	0	0	V	1	1	1
<u>Eremias</u>	1	0	0	1	0	1	1	-	-	V	0	V	0	0	V	V	V	1
<u>Pedioplanis</u>	1	0	0	0	0	V	V	-	-	0	0	0	0	0	1	V	1	1
<u>Meroles-Aporosaura</u>	1	0	0	V	0	V	V	-	-	0	0	V	0	0	1	V	1	1
<u>Pseudieremias</u>	1	0	0	1	0	1	1	-	-	0	0	0	0	0	1	1	1	1
<u>Heliobolus</u>	1	0	0	1	0	1	1	-	-	0	0	V	0	0	1	1	1	1
<u>Ichnotropis</u>	1	0	0	1	1	1	1	-	-	0	0	0	0	0	1	1	1	1
<u>Latastia</u>	1	0	0	1	0	1	1	-	-	0	0	V	0	0	0	1	1	1
<u>Philochortus</u>	1	0	0	1	V	1	1	-	-	0	1	0	0	0	1	1	1	1
<u>Nucras</u>	V	0	0	1	V	1	1	-	-	0	0	0	0	0	1	1	1	1
<u>Poromera</u>	1	0	0	1	1	1	0	-	-	0	0	0	0	0	1	1	1	1
<u>Tropidosaura</u>	1	0	0	1	V	1	1	-	-	V	0	0	0	0	1	-	-	1
<u>Holaspis</u>	1	0	0	0	0	1	1	-	-	1	0	0	0	0	1	1	1	1
' <u>Lacerta</u> ' <u>australis</u> etc	-	-	-	0	0	1	1	-	-	1	0	0	0	-	-	1	V	1
<u>Gastropholis</u>	1	0	0	1	1	1	1	-	-	0	0	0	0	0	1	1	1	1
<u>Bedriagaia</u>	1	0	1	1	1	1	1	-	-	0	1	0	0	0	1	1	1	1
' <u>Lacerta</u> ' <u>echinata</u>	1	0	1	1	0	1	1	-	-	0	1	0	0	0	1	1	1	1
<u>Adolfus alleni</u>	1	0	0	0	0	1	1	-	-	0	0	0	0	0	1	1	1	1
<u>Adolfus africanus</u> etc	1	0	0	0	0	1	1	-	-	0	0	0	0	0	1	V	1	1
' <u>Lacerta</u> ' <u>jacksoni</u>	1	0	0	0	0	1	1	-	-	0	0	0	0	0	1	1	1	1
<u>Takydromus</u> etc	0	1	0	V	0	0	0	1	0	-	0	0	0	0	1	0	0	0
<u>Gallotia</u>	0	0	0	V	0	0	0	1	0	-	0	0	1	0	1	0	0	0
<u>Psammmodromus algirus</u>	0	0	0	0	0	0	0	1	1	-	0	0	0	0	1	0	1	0
<u>Psamm. hispanicus</u> etc	0	0	0	0	0	0	0	0	0	-	0	0	1	1	0	0	0	0
<u>Lacerta parva</u> etc	0	0	0	0	0	0	0	0	0	-	0	0	0	1	0	1	0	0
<u>Lacerta brandtii</u>	1	0	0	0	0	0	0	0	0	-	0	0	0	-	-	0	0	0
<u>Podarcis</u>	0	0	0	0	0	0	0	1	1	-	0	0	0	0	1	0	1	0
<u>Lacerta andreanszkii</u>	1	0	0	1	0	0	0	0	1	-	0	0	0	0	1	0	0	0
<u>Lacerta perspicillata</u>	0	0	0	0	0	0	0	0	1	-	0	0	0	0	1	0	0	0
<u>Lacerta dugesii</u>	1	0	0	0	0	0	0	0	0	-	0	0	0	0	1	0	0	0
<u>Lacerta danfordi</u> etc	0	1	0	0	0	0	0	1	1	-	0	0	0	0	0	0	0	0
<u>Lacerta laevis</u>	1	0	0	0	0	0	0	0	1	-	0	0	0	0	0	0	0	0
<u>Lacerta</u> , <u>archaeolacertas</u>	V	0	V	0	0	0	0	0	0	-	0	0	0	0	V	0	0	0
<u>Lacerta oxycephala</u>	0	0	1	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0
<u>Lacerta graeca</u>	0	0	1	0	0	0	0	0	0	-	0	0	0	0	1	0	0	0
<u>Algyroides</u>	0	0	0	0	0	0	0	0	0	-	0	0	0	0	V	0	0	0
<u>Lacerta cappadocica</u>	0	1	1	0	0	0	1	0	0	-	0	0	0	0	1	0	0	0
<u>Lacerta agilis</u> etc	1	0	0	0	0	0	0	0	0	-	0	0	0	0	V	0	0	0
<u>Lacerta princeps</u>	1	0	0	0	0	0	0	0	0	-	0	0	0	0	1	0	0	0
<u>Lacerta lepida</u> etc	1	0	0	1	0	0	0	0	0	-	0	0	0	0	1	0	0	0
<u>Lacerta jayakari</u> etc	1	0	1	0	0	1	1	-	-	0	0	0	0	0	V	0	0	1
<u>Lacerta vivipara</u>	0	1	0	0	0	1	1	-	-	0	0	0	0	0	0	0	0	0
Hypo. Ethiopian ancestor	1	0	0	0	0	1	1	-	-	0	0	0	0	0	0	1	1	1

Appendix 2 (part g)

	81-2	82	83	84
Ancestor	0	0	0	0
<u>Ophisops-Cabrila</u>	1	0	0	0
<u>Mesalina</u>	1	0	0	V
<u>Acanthodactylus</u>	1	0	0	0
<u>Eremias</u>	1	0	0	0
<u>Pedioplanis</u>	1	0	0	0
<u>Meroles-Aporosaura</u>	1	0	0	V
<u>Pseudieremias</u>	1	0	0	0
<u>Heliobolus</u>	1	0	0	0
<u>Ichnotropis</u>	1	0	V	0
<u>Latastia</u>	1	0	0	0
<u>Philochortus</u>	1	0	0	0
<u>Nucras</u>	1	0	0	0
<u>Poromera</u>	1	0	0	0
<u>Tropidosaura</u>	1	0	0	0
<u>Holaspis</u>	1	0	0	0
' <u>Lacerta</u> ' <u>australis</u> etc	1	-	0	-
<u>Gastropholis</u>	1	0	0	0
<u>Bedriagaia</u>	1	0	0	0
' <u>Lacerta</u> ' <u>echinata</u>	0	0	0	0
<u>Adolfus alleni</u>	0	0	0	0
<u>Adolfus africanus</u> etc	V	0	0	0
' <u>Lacerta</u> ' <u>jacksoni</u>	0	0	0	0
<u>Takydromus</u> etc	0	0	0	0
<u>Gallotia</u>	0	1	1	1
<u>Psammodromus algirus</u>	0	1	1	1
<u>Psamm. hispanicus</u> etc	0	0	1	1
<u>Lacerta parva</u> etc	0	0	0	0
<u>Lacerta brandtii</u>	0	0	0	0
<u>Podarcis</u>	0	0	0	0
<u>Lacerta andreanszkii</u>	0	0	0	0
<u>Lacerta perspicillata</u>	0	0	0	0
<u>Lacerta dugesii</u>	0	0	0	0
<u>Lacerta danfordi</u> etc	0	0	0	0
<u>Lacerta laevis</u>	0	0	0	0
<u>Lacerta, archaeolacertas</u>	0	0	0	0
<u>Lacerta oxycephala</u>	0	0	0	0
<u>Lacerta graeca</u>	0	0	0	0
<u>Algyroides</u>	0	0	0	0
<u>Lacerta cappadocica</u>	0	0	0	0
<u>Lacerta agilis</u> etc	0	1	0	0
<u>Lacerta princeps</u>	0	1	0	0
<u>Lacerta lepida</u> etc	0	1	0	0
<u>Lacerta jayakari</u> etc	1	0	0	1
<u>Lacerta vivipara</u>	0	0	0	0
Hypo. Ethiopian ancestor	0	0	0	0